Czech University of Life Sciences in Prague

Faculty of Forestry and Wood Sciences

Disturbance dynamics of mountain temperate primary forests of the Western and Southern Carpathians and its effect on forest structure and bird assemblages

Doctoral thesis

Study programme: Forestry Engineering

Field of study: Forest Biology

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Advisor: Ing. Martin Mikoláš, PhD.

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Faculty of Forestry and Wood Sciences

Ph.D. THESIS ASSIGNMENT

Mgr. Ondrej Kameniar

Forestry Engineering

Forest Biology

Thesis title

Disturbance dynamics of mountain temperate primary forests of the Western and Southern Carpathians and its effect on forest structure and bird assemblages

Objectives of thesis

Understanding the historical disturbance regimes of the remaining primary forests and its influence on current forest structure and biodiversity is crucial for the conservation, sustainable forestry and for predicting possible trajectories of future forest ecosystem development in the region. Beech- and spruce-dominated forests are the most common forest types in mountains of Central Europe. They are naturally occurring in neighbouring altitudinal belts, but were studied separately – studies from single unfragmented, large-scale primary forest landscape are missing. Therefore, there is also a lack of information about disturbance synchronisation between these forest types. Birds (Aves) participate in many inevitable ecological processes such as deadwood decomposition, seed dispersal and herbivore insect control. Thus, they are an important part of native forest biodiversity. Additionally, they are sensitive to changes in environmental structure and easy to record and identify. Due to their large area requirement, they serve as umbrella species – safeguarding their populations can help to protect significant part of the overall native biodiversity. Our results are aimed to help forest management and nature protection to promote biodiversity in forest ecosystems.

Particular aims of the thesis are:

1. Describe the historical disturbance regime with the focus on disturbance synchronisation, in primary forest landscape, which is containing beech and spruce forest type.

2. Investigate the influence of historical disturbances in spruce-dominated primary forests on forest structure and bird assemblages.

3. To compare the forest structure and bird assemblages' composition in beech- and spruce-dominated primary forests.

Methodology

The study will take place in the primary spruce- and beech-dominated forests in the Western and Southern Carpathian Mountains. Sample plots will be selected from the network of permanent research plots previously established using stratified random design. Field data will be collected to describe disturbance history, forest structure and breeding bird assemblages. We will use a dendrochronological approach to reconstruct and describe the spatiotemporal patterns of historical disturbances. To analyse synchronicity

of disturbances we will use the Kendall's coefficient of concordance – W. Regression analysis will be employed to assess the differences in stand-level synchrony between beech- and spruce-dominated forests. To analyse the influence of disturbance history on structure and bird assemblages, we will calculate diversity indices for description of bird assemblages and we

will characterize plot level bird communities using density and diversity of bird species per plot. Generalized linear mixed models (GLMM) will be used to relate overall abundance, richness, and Shannon diversity of bird assemblages to forest structural characteristics. Distance-based partial redundancy analysis (db-pRDA) will be used to evaluate the influence of forest structure on bird assemblage composition.

The proposed extent of the thesis

100
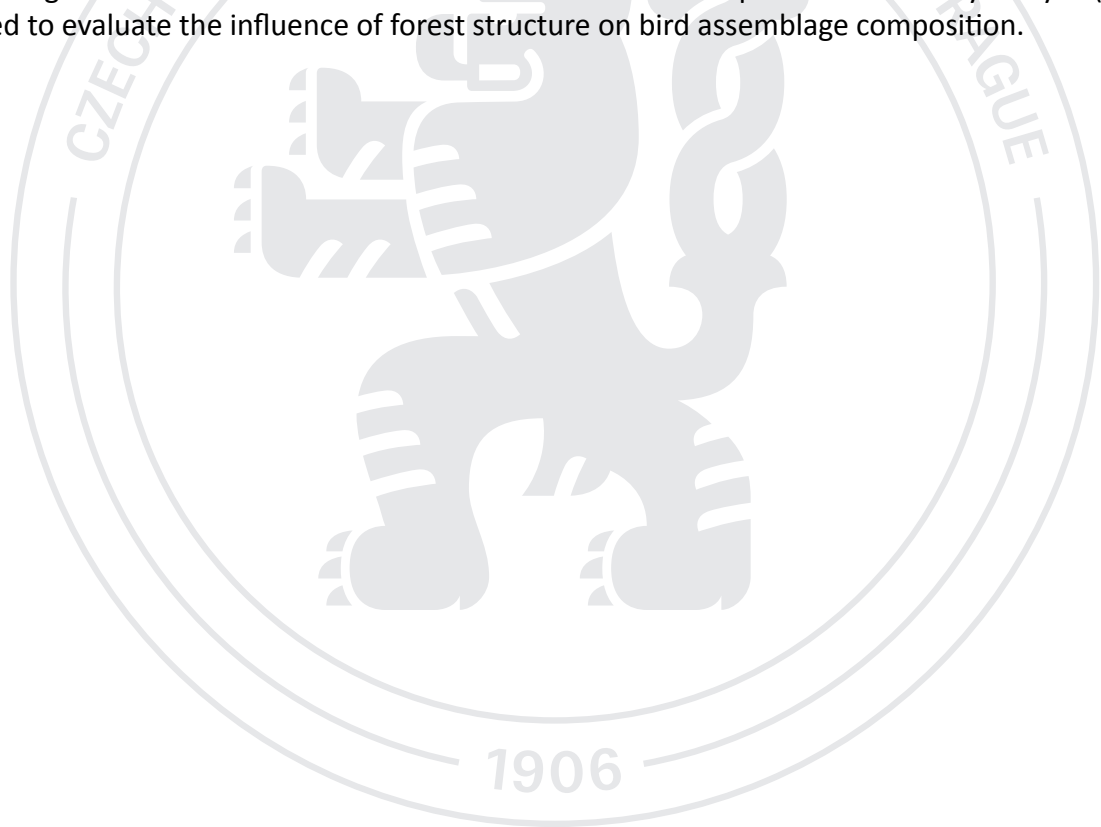
Keywords

Primary forest, natural disturbances, disturbance synchronisation, beech, spruce, forest structure, birds, Carpathians

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I hereby confirm that this PhD. thesis "Disturbance dynamics of mountain temperate primary forests of the Western and Southern Carpathians and its effect on forest structure and bird assemblages" was elaborated independently with the usage of quoted literature and based on consultations and the recommendations of my supervisor.

I agree with publishing this PhD. thesis according to Czech law n. 111/1998 Sb. about the universities in its current valid wording. This agreement is independent from the results of defense.

December 31th, 2022, Liptovský Mikuláš

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The six-year journey leading to the writing of this dissertation is at the end. At the beginning, I had no idea how much new knowledge, adventurous days and nights in the wildest corners of European nature, but also endless hours in the laboratory or at the computer my PhD studies would bring me. Thanks to God, everything fell into place and the result is this dissertation.

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Abstract

Understanding temporal and spatial variations in historical disturbance regimes, dynamics of forest structure and their impact on forest species across primary forest landscapes is imperative to help forecast forest development and adapt forest management in an era of rapid environmental change. Mountain spruce- and beech-dominated forests are forest communities of major importance in temperate Europe. However, information on the differences between their historical disturbance regimes, structures, and biodiversity from complex primary forest landscapes is still incomplete. In order to evaluate the impact of natural disturbances and forest structure on temperate mountain primary forest biodiversity, we established ～300 permanent study plots in the best preserved mountain primary forests in the Western and Southern Carpathian Mountains. Our dataset combines disturbance history variables, forest structural variables (forest density, tree diameter distribution, tree height, tree age, tree-related microhabitats, deadwood quantity and quality, regeneration) and breeding bird counts. We selected birds as the model group, because they are an important part of forest biodiversity, sensitive to different aspects of forest structure and contain well known indicator and umbrella species.

First, using a tree-ring-based approach, we describe 250 years of historical disturbance regime with the focus on disturbance synchronisation in primary beech- and spruce-dominated forest landscape (Section 5.1). Second, we used birds as a model group to investigate the influence of historical disturbances in spruce-dominated primary forests on forest structure and bird assemblages (Section 5.2). As a last step, we compared the forest structure and bird assemblages' composition in beech- and spruce-dominated primary forests (Section 5.3).

The main findings of this thesis are:

i)   Synchronised disturbances with higher severity were infrequent but critical as drivers of subsequent dynamics across beech- and spruce-dominated primary forest stands within the largest preserved mountain primary forest landscape in temperate Europe. High-severity disturbances were synchronised across both forest types at the landscape scale, while moderate- and low-severity disturbances were asynchronous and random in both spruce- and beech-dominated primary forests. We detected a peak of canopy disturbance across the region at the end of the nineteenth century. Spruce forests had significantly higher average synchrony and higher between-stand variability of synchrony than the beech-dominated forests (Section 5.1).

ii)   Bird assemblages were significantly influenced by forest structure which was in turn shaped by disturbance dynamics (disturbance frequency, time since the last disturbance and its severity). Early-successional species associated with more open habitats were positively influenced by disturbance-related structure, while some species responded negatively. At the same time, overall abundance, species richness and Shannon diversity of the bird assemblage remained unchanged under variable disturbance histories (Section 5.2).

iii)   Differences in the forest structure in beech- and spruce-dominated primary forests supported significantly different bird community compositions among these two forest types. Spruce-dominated primary forest had a higher density of cavities and higher canopy openness, while higher tree species richness and more intense regeneration was found in beech-dominated primary forests. Bird assemblages showed higher species richness in beech-dominated primary forests, but lower total abundance. The majority of bird species which occurred in both forest types were more numerous in spruce-dominated forests, but more species occurred exclusively in beech-dominated forests. Further, some spruce-preferring species were found in naturally disturbed patches in beech-dominated primary forest. High forest age, high standing and downed deadwood volumes and multiple tree-related microhabitats provide important habitat opportunities for numerous rare bird species in both forest types (Section 5.3).

Our results provide valuable insight into forest dynamics and bird assemblages in spruce- and beech-dominated mountain temperate forests in the Carpathians. We suggest that management efforts should recognize protecting large continuous and altitudinally diversified forest landscapes as a necessary measure to ensure the temporal and spatial structural heterogeneity which is driven by a wide range of disturbances, and thereby provide habitat opportunities for numerous species. The diverse and synchronous disturbance activity among two interconnected forest vegetation types highlights the need for complex spatiotemporal forest management approaches that emulate disturbance synchronicity to foster bird assemblages diversity across multiple forest vegetation types within forest landscapes. Thus, protecting existing primary forests, allowing managed forests to attain older ages, and increasing the heterogeneity and availability of primary forest structures in the landscapes are necessary to maintain diverse beech and spruce forest communities in times of accelerating environmental change.

Key words: dendroecology, natural disturbances, forest structure, beech, spruce, birds, primary forest, Carpathians

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List of abbreviations

BDPF – beech-dominated primary forests

CO_2 – carbon dioxide

DBH – diameter in breasts height

Db-pRDA – Distance-based partial redundancy analysis

db-RDA – distance-based redundancy analysis

E – East

EU – European Union

FAO – Food and Agriculture Organisation

Fig. – Figure

GAM – Generalized additive models

GIS – geographic information system

GLMM – Generalized linear mixed model

LASSO – least absolute shrinkage and selection operator penalty

Mg – Mega gramme

Mha – millions of hectares

N – North

NGO – Non-governmental organisation

pRDA – Partial redundancy analysis

REMOTE – REsearch on Mountain Temperate primary forests

SDPF – spruce-dominated primary forests

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USD – United States Dollar

WWF – World Wildlife Fund

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1 Introduction

Primary forests and forests with high naturalness are refugia for native biodiversity, provide essential ecosystem services, and serve as reference areas for sustainable forest management (Keeton 2007, Wirth *et al*. 2009, Watson *et al*. 2018). As the pace of climate change continues to increase, primary forests also promise higher resilience to increasing climate extremes compared to forest plantations and landscapes modified by human management (Thompson *et al*. 2009, Pettit *et al*. 2021, Feng *et al*. 2022, Potterf *et al*. 2022). In recent decades, primary forests have also emerged as reference ecosystems for managed forests (Kuuluvainen and Aakala 2011) and are important sources of long-term historical data about forest dynamics and development (Luick *et al*. 2021a). In contrast to managed forests with strong anthropogenic influences, primary forests are shaped by natural processes, including natural disturbances (Pickett and White 1985, Nagel *et al*. 2013, Svoboda *et al*. 2014). A natural forest disturbance is any discrete event resulting in tree mortality, which can occur at differing severities and spatial extents (White and Pickett 1985). It can be caused by abiotic (e.g. windstorms, ice storms, and drought) and biotic (e.g. insects, pathogens, and herbivores) factors (Kulakowski *et al*. 2016). In recent decades, the frequency and extent of natural disturbances have increased throughout forests around the world (Turner 2010, Seidl *et al*. 2014). Shifting disturbance regimes are impacting not only commercial forest plantations but also large areas of primary and natural forest fragments within protected areas (Sommerfeld *et al*. 2018, Potterf *et al*. 2022). In particular, large-scale and high-severity disturbances have provoked heated debates about the "naturalness" of such events and appropriate management responses (Lindenmayer *et al*. 2017, Potterf *et al*. 2022). Although we have detailed depictions of the disturbance history of various remnants of primary temperate forests (e.g., Splechtna *et al*. 2005, Janda *et al*. 2014, Trotsiuk *et al*. 2014), there is a scarcity of similar information from intact, continuous, and altitudinally diverse primary forest landscapes, which would enable the analysis of disturbance regime histories and synchronicity between different forest community types.

Contemporary ecology recognizes the fundamental role of natural disturbances and tree mortality processes in the dynamics of forest structural development and thus habitat availability for the full range of biodiversity associated with different successional stages (Franklin *et al*. 2002, Holeksa *et al*. 2007, Nagel *et al*. 2013, Battisti *et al*. 2016). Birds (Aves) are a vital ecosystem

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element, participating in processes such as decomposition, pollination and seed dispersal (Sekercioglu *et al*. 2004). As they have relatively large spatial requirements (Whelan *et al*. 2015) extensive forest areas are needed to keep their populations viable. Safeguarding habitat for birds can thus be a helpful approach for effective ecosystem and biodiversity management (Suter *et al*. 2002, Mikoláš *et al*. 2015, Thom and Keeton 2020). Previous research has shown that birds are highly sensitive to changes in forest structure (Dunlavy 1935, MacArthur and MacArthur 1961, Cody 1985, Baláž and Kocian 2015), because it influences many aspects of bird ecology including food supply, predation risk, and breeding site availability (Brawn *et al*. 2001, Hanzelka and Reif 2016). However, the relationships of disturbance history, forest structure and bird assemblage composition remain insufficiently explored in Norway spruce and European beech forests.

Dendrochronological methods are a useful tool to gain high resolution and long-term data on the disturbance history of temperate forests (Lorimer and Frelich 1989). The relationships between historical disturbance events and biodiversity operate through the effects of disturbances on forest structural conditions and successional dynamics (Mikoláš *et al*. 2017b). These, in turn, directly influence biodiversity, for instance through controls on the availability of seral habitats, stand density and canopy cover, and key structures such as standing and downed dead trees (Kameniar *et al*. 2021). However, because it is a highly laborious process to obtain dendrochronological disturbance history data, previous studies have mainly focused on immediate or relatively short-term impacts of natural disturbances on bird assemblages (Beudert *et al*. 2015, Thorn *et al*. 2016, Kortmann *et al*. 2018). There is still a lack of scientific literature regardings information on the long-term influence of particular disturbance traits like severity, frequency and timing on birds.

The global biodiversity crisis became, along with the climate crisis, a major issue of our times (IPCC 2022, IPBES 2019). Forest management as a human activity, which is influencing a significant part of the Earth surface, can be an important part of the solution of these interconnected challenges (Verkert *et al*. 2022). However, it needs to be based on the best-as-possible information. The results presented in this thesis aims to improve our knowledge about the functioning of primary temperate forest ecosystems and to help forest management to maintain the whole array of native biodiversity.

2 Literature review

2.1 Primary forests - definition, area, importance, and protection

Forests are natural ecosystems covering large parts of Earth's terrestrial surface (FAO 2020). However, since the agricultural revolution, they are rapidly shrinking; in the last 300 years, Earth has lost around 35% of natural forests, almost exclusively due to human activity (Mackey *et al*. 2015). Actual forest cover is estimated to be around 4,06 billion hectares, around 31% of land surface (FAO 2020). However, the majority of this area has been altered to some extent (Watson *et al*. 2018). This is especially true for Europe; the smallest and most densely populated continent with a long history of intensive human activities (Sabatini *et al*. 2018).

To date, only a tiny fraction of European forests escaped destruction or significant alteration by forest management or regenerated to a state close to natural (Sabatini *et al*. 2021). The exact area of such preserved forests depends on the definition and level of naturalness which we consider. The degree of naturalness is a continuum with many possible states, therefore, it is understandable that a vast number of sometimes ambiguous and synonymous terminology has evolved. In English-language scientific literature, the most common expressions referring to the best-preserved remnants of original forests are: *primaeval*, *intact*, *undisturbed*, *untouched*, *old-growth* and *virgin* forests (for a more detailed discussion, see Križová 2011, Luick *et al*. 2021 and Vandekerkhove *et al*. 2022). However, their meaning is not identical. We prefer to use the term *primary forests*. One reason is that this term is also preferred by FAO (2015, 2020), which defines primary forests as naturally regenerated forests of native species with no clearly visible indications of direct human impact, and where ecological processes have not been significantly disturbed. On the other hand, the other aforementioned terms are less suitable in the context of our research.

A frequently used term is "old-growth forest". However, its meanings are very diverse, and depends on geographical area. Generally, it refers to the developmental stage of the forest, which consists of old trees, but it can also be a secondary forest (Vandekerkhove *et al*. 2022). It is not necessarily a result of natural processes and does not necessarily consist of a naturally occurring mix of species. It is often a formerly managed stand, which was left for spontaneous development. The structural characteristics (e.g. deadwood amounts, canopy heterogeneity, tree species

composition, DBH diversity, overall biodiversity) remain strongly altered compared to a primary forest (Commarmot *et al*. 2005). It is often the case in Western European forest reserves, where primary forests are missing almost without exception, whilst this is not the case in other parts of Europe (Sabatini *et al*. 2018, 2021); the largest concentration of preserved primary forest in temperate Europe are found in the Carpathian Mountains (Sabatini *et al*. 2019, Luick *et al*. 2021a). Primary forest typically comprises patches of all developmental stages, and the old-growth stage is only one of them. Young naturally regenerating patches after a windstorm or other natural disturbance can also be primary forest (Sabatini *et al*. 2018). It is important to stress this difference because confusion about primary and old-growth forests can lead to incorrect results and harmful management implications (Luick *et al*. 2021a).

We also do not use terms as a *virgin* (Veen *et al*. 2010), *untouched* (Parviainen *et al*. 2000), *intact* (Watson *et al*. 2018, Moomaw *et al*. 2019)*, and *undisturbed by man* (Forest Europe 2015, 2020). Research in the last decades has shown that many forest landscapes, traditionally viewed as untouched, were, in fact, shaped by human activities for a long time. The classic example is the Amazonian rainforest, where local tribes intentionally modified species composition in systems more similar to sustainably managed agroforestry systems than to untouched wilderness (Barlow *et al*. 2012). The same is true for many Northern American forest areas (Anderson *et al*. 1997, Klimaszewski-Patterson and Mensing 2020). The situation is even more complicated in densely populated Europe. Historically, most probably all forests and ecosystems were in some way subject to more or less intensive use. Despite that, some fragments of original *primary* forest - although probably not *untouched* - remained until today, even in the Central and Southeastern European mountains, which are the focus of our study (Mikoláš *et al*. 2021).

Although direct visible human influence on primary forests is possible to exclude to a great extent, there is still indirect influence, which is currently globally present as we entered the Anthropocene (Guz and Kulakowski 2020). Primary forests are influenced by human-induced climate change, changing species composition (trees and other parts of biodiversity) and changing disturbance regimes (Sommerfeld *et al*. 2018, McDowell *et al*. 2020). These influences are amplified in more fragmented forests (Laurance and Williamson 2001). A good example is the spreading of bark beetles from the forest edges created by salvage logging or other forest management practices (Kautz *et al*. 2013). Primary forests are also indirectly influenced by the absence of large fauna, such as large ungulates including aurochs (*Bos primigenius*), European

bison (*Bison bonasus*) and other species of so-called *megafauna.* They acted like disturbance agents - reducing forest regeneration and maintaining meadows (Ivanova *et al*. 2018, Sandom *et al*. 2014). In Western Europe, primary forests are also impacted by the absence of large predators like the wolf (*Canis lupus*), lynx (*Lynx lynx*), and bear (*Ursus arctos*), which results in overgrazing by herbivores (Šebková *et al*. 2011). In the primary forests of the Western and Southern Carpathians, the focus of our study, large predators are still present, sometimes even in high population densities (Straka *et al*. 2012).

Both, spruce- and beech-dominated primary forests in the Carpathians are typically characterised by vertically and horizontally heterogeneous structure (Commarmot *et al*. 2005, Rodrigo *et al*. 2022). In regard to vertical structuring, a typical stand contains moss, plants, shrubs, and tree regeneration of different heights, in addition to several layers of canopy, including very large and tall trees, and standing dead and dying trees of different sizes and decay stages of deadwood, typically in high quantities. Horizontally, a primary forest is a mosaic of patches with varying structure – in terms of DBH, age, tree dimensions, amount of deadwood and other parameters (Korpeľ 1989, Gilg 2005, Kozák *et al*. 2021, Vandekerkhove *et al*. 2022). Typically, patches are finer due to the prevailing single to several trees' mortality gaps (Drössler and von Lupke 2005, Čada *et al*. 2020, Frankovič *et al*. 2021). However, larger patches up to several or tens of hectares were also identified in spruce- (Čada *et al*. 2020) and beech-dominated primary forests in the Carpathian Mountains (Feldmann *et al*. 2018). Needless to say, natural disturbance-induced gaps in managed forests, with their simplified horizontal and vertical structure, often reach a magnitude of larger areas (Kunca *et al*. 2014, Nagel *et al*. 2016). The disturbance regime of beech and spruce-dominated primary forests is described in more detail in chapter 2.2.

According to the official European forestry statistics, there is 227 million ha of forested land in Europe, excluding the European part of the Russian Federation - more than one-third of Europe, (Forest Europe 2020). Only a tiny proportion of this area is still in its primary state. Despite the enormous importance of these remnants of the original forest ecosystem, the exact areas of primary forests are still unknown. Information sources estimate considerably different numbers: according to the latest research (Sabatini *et al*. 2021), it is around 0.6% (3.7Mha) of European forests, but official European forestry statistics claim it is 2.2% (Forest Europe 2020). There is also a severe contradiction between forestry reports and independent research regarding current trends in primary forests area; while research reports a significant ongoing loss of primary forests in the

last decades (Hansen *et al*. 2013, Luick *et al*. 2021a), official forestry data report a large increase – 42.3% in the last 30 years (Forest Europe 2020). However, it is hard to explain such a large increase in primary forest area considering 7,3 Mha (4% of European forests) was identified in a report published five years earlier (Forest Europe 2015).

Europe's best-preserved continuous forest areas are found in the Carpathian Mountains, which host around 80% of the European Union's temperate primary forests (Luick *et al*. 2021a). The primary forests in the Slovakian Carpathians were precisely mapped recently; they spread over 10,583 ha, which amounts to 0.47% of Slovakia's forests (Jasík and Polák 2011, Mikoláš *et al*. 2019). The area is generally stabilised, but a loss of 163 ha has been documented since the inventory (Mikoláš *et al*. 2019). In December 2021, the nature reserve "Primary forests of Slovakia" was established to protect all state-owned primary forests with their surroundings, which, prior to this new state legislation, lacked strict protection. Currently, 94.5% of primary forests are strictly protected, and only some privately owned parcels have lower degrees of protection. Only 159 ha are totally without protection.

The situation in Romania, the second focus country of this research, is much less clear, partly because of the significantly larger area of forests and primary forests. According to the latest inventory, based on an analysis of current and historical aerial photos, there is potentially more than 525,000 ha of primary and old-growth forests (Schickhofer and Schwarz 2019). Other estimates are around 200,000 ha (WWF 2016). Compared with Slovakia, the situation in Romania is much more dynamic – primary and old-growth forests are still logged at a very high pace, often illegally, and often by wood-processing companies from the EU (Environmental Investigation Agency 2015). NGOs estimate that during 2001 – 2019 alone, Romania lost about 350,000 ha of forests (Global Forest Watch 2020), including large areas of primary and old-growth forests. Even the largest clusters of primary forests located in the Făgăraș Mountains did not escape this degradation. We are witnessing large-scale logging in previously untouched areas (Spînu *et al*. 2021, Luick *et al*. 2021a), including research plots established for the purpose of our research. However, official forestry statistics claim that the area of primary forests in Romania increased from 128,000 to 165,000 ha in the period 1990 – 2020 (Forest Europe 2020). Romania formally protects its primary forests through the "Romanian National Catalogue of Virgin and Quasi-virgin Forests". Despite the actual protection of more than 70,000 ha, most of the valuable forests remain unprotected and are directly threatened by logging. The main reason offered is a policy that permits

salvage logging of areas recently affected by natural disturbances (Spînu *et al.* 2021). When we consider that for decades, scientific research has provided proof that primary forests are shaped by natural dynamics, including natural disturbances, the motives behind such reasoning are highly questionable (Lindenmayer *et al.* 2017).

The ongoing destruction of primary and other natural forests in Europe is a severe problem, especially in combination with attempts to hide it in official statistics. While the importance of forests is relatively well accepted in society, there still needs to be more awareness about the unique role of forests with high naturalness (Watson *et al.* 2018, Luick *et al.* 2021a). In general, forests with higher naturalness are better at provisioning ecosystem functions and creating habitat for native biodiversity, and they represent the full potential of forest functionality (Watson *et al.* 2018). Intensively managed even-aged and single-species plantations, common in Central Europe, are on the other side of the naturalness scale - their ecology is altered to such an extent that some authors do not consider them a forest (DellaSala 2019).

Therefore, the protection of primary forests should be a priority, especially in the context of the recent onset of rapid climate change (Mackey *et al.* 2015, DellaSala *et al.* 2020, Kun *et al.* 2020, Sabatini *et al.* 2020). In comparison with less natural forests, they promise higher resilience to increasing climate extremes compared to forest plantations and landscapes modified by human management and land uses (Thompson *et al.* 2009, Pettit *et al.* 2021). It is caused by primary forest heterogeneity – they contain patches which react to disturbances differently. Partly it is because the patches differ in age and vertical structure and are composed of different species (Sommerfeld *et al.* 2020). Another reason the primary forest is more resilient than simplified production forests is that there are uninterrupted symbiotic connections, most notably between trees and fungi (Beiler *et al.* 2009, Pickles and Simard 2017).

Moreover, primary forests store vast amounts of carbon in large living trees, deadwood and, most importantly, in soil (Luick *et al.* 2021b, Meyer *et al.* 2021). In the case of temperate forests, it is always significantly higher than in managed forests (Keith *et al.* 2014). Recent research has found that large trees in spruce primary forests react to higher average temperatures by increased radial growth (Begović *et al.* 2022), and the same trend was reported for saplings (Marchand *et al.* 2023). This means that the overall carbon sink potential is probably not decreasing with climate change, as suggested before (Odum 1969). If primary forests are affected by logging, the majority of carbon is released back into the atmosphere, and carbon fixed in long-lived wood products does

not compensate for this loss (Luick *et al*. 2022). On the contrary, when previously managed forests are protected and allowed to regenerate to their full natural potential (so-called proforestation), they accumulate large quantities of carbon (Meyer *et al*. 2021). In addition, other ecosystem services (conservation of biodiversity, water and air quality, flood and erosion control, public health benefits, low-impact recreation, and scenic beauty) are also enhanced (Moomaw *et al*. 2019). It is estimated that *natural climate solutions* (the restoration of forests and other natural ecosystems, together with regenerative agriculture and other activities) can provide 37% of cost-effective CO_2 mitigation needed by 2030 for a >66% chance of holding warming below 2°C, while one-third of this cost-effective mitigation can be delivered at or below 10 USD per Mg of CO_2 (Griscom *et al*. 2019).

2.2 Natural disturbances in mountain forests

The perception of natural ecosystems has changed significantly over the last decades, where the idea of "equilibrium in nature" has gradually been replaced by the concept of continuous change (Pickett and White 1985). This resulted in a fundamental change in the understanding of natural systems, their disturbances and overall functioning. Mountain temperate primary forests are not long-term static environments – they undergo changes at different spatial levels across various time scales. When looking at a more extended period of time (hundreds to thousands of years), an ongoing adaptation to climate changes occurs (Nagel *et al*. 2013). In today's era of rapid global environmental change, such adaptive responses have already been observed over much shorter periods of time (Turner 2010, Parobeková *et al*. 2018, Seidl *et al*. 2017). However, over short time intervals, the decisive factor shaping the structure of forest ecosystems are natural disturbances – time-limited events of variable intensity, during which tree mortality occurs in some areas (Angelstam and Kuuluvainen 2004). Disturbances change resource availability and disrupt an ecosystem or community (Pickett and White 1985, Mikoláš *et al*. 2021). Regularly repeating sequence of disturbances of different strengths and characters in a given territory over time with certain variability can be characterised as a disturbance regime (Frelich 2002). Disturbance regimes can be described by the spatial distribution of disturbances, their intensity, severity, frequency, return interval and size (Turner 2010).

Recently, there has been a significant shift in understanding the character of natural disturbances in the Central European mountain forests. Even in the recent past, there were two

competing hypotheses. One hypothesised that only small-scale, so-called gap dynamics occur in stands undisturbed by humans, caused by the mortality of one or several trees (Korpeľ 1989). According to it, all forests are naturally progressing through different successional stages toward climax, which is the stage with restored "natural balance". The other hypothesis only considered large-scale events as important, following the pattern of Nordic spruce forests (Kuuluvainen and Aakala 2011). Today, disturbances are understood as temporally and spatially highly variable events of varying intensity, from the death of one tree as a result of competition, pathogens or age through the death of a larger group of trees, to catastrophic landscape-scale disturbances (Pickett and Write 1985, Nagel *et al.* 2013, Battisti *et al.* 2016). Disturbance can also take the form of scattered mortality, spread over a larger area (Čada *et al.* 2020). The impact of different events is partly overlapping, and together they create a fine mosaic of developmental stages. Many biotic and abiotic agents cause disturbances: bark or leaf-eating insects, fungi, large mammalian herbivores, fire, wind, frost, drought, avalanche, landslide or flood (Pickett and White 1985, Turner 2010, Kulakowski *et al.* 2016, Seidl *et al.* 2017). Often, several factors occur simultaneously which can amplify the resulting disturbance. The most typical case is drought - visible tree damage is often the product of bark beetles or wind, but trees are already weakened by one or more seasons of lower precipitation which thus facilitated subsequent damage by other disturbance agents (Wermelinger 2004, Schurman *et al.* 2018, Leuschner 2020).

One of the key aspects of disturbance that influences further successional development, structure, biodiversity and thus habitat resilience is the emergence of so-called biological legacies. As defined by Franklin *et al.* (2000), these are all organisms, organic material and organically created environmental structures persisting through a disturbance, which are subsequently incorporated into a recovering ecosystem. In the forest environment, this is mostly dead wood in various stages of decomposition and positions, for example, standing broken trunks, lying logs, and dead branches. Disturbance disrupts tree dominance and quickly frees up space and resources for various organisms, including a new generation of trees (Swansson *et al.* 2011). The problem is when this stage of forest development is seen as a catastrophe that can only be solved by clear-cutting the affected area - so-called salvage logging - which removes most of the indispensable biological heritage. The impact of this practice on biodiversity has been summarised by Thorn *et al.* (2017).

Global climate change is increasingly identified as the most severe factor which has led to a shift in disturbance regimes of forest ecosystems worldwide (Schelhaas *et al*. 2003, Seidl *et al*. 2017). It is likely interfering with multiple factors such as artificial simplification of forests, air pollution, the spread of nonnative or invasive species and other predominantly anthropogenic stressors, and so-called mega disturbance events are also occurring (Millar and Stephenson 2015). In recent years, many places across the world have experienced catastrophic disturbances as a consequence of climate-related droughts and ongoing direct human pressures on local ecosystems (Troumbis *et al*. 2021, Neary *et al*. 2022). Among the most severe and widespread were wildfires in Australia (Clarke *et al*. 2015, Collins *et al*. 2021), Russian Siberia (Kharuk *et al*. 2021), California (Keeley and Syphard 2021), and the Amazon (Xu *et al*. 2020), and insect outbreaks in multiple coniferous ecosystems from Mexico to Canada in North America (Bentz *et al*. 2009) and southern Siberian fir forests (Debkov *et al*. 2019).

Similarly, forest disturbances are becoming more frequent in Europe, and their scale has been expanding for the last two centuries (Seidl *et al*. 2014). Increased intensity and frequency of disturbances can be seen as an opportunity to increase the adaptability of ecosystems - with each disturbance, long-standing unchanged patches are removed and replaced with those best adapted to the current situation. Thus, it can be said that the more frequent the disturbances are, the more often the ecosystem has the opportunity to "update itself" to changing climatic conditions (Thom *et al*. 2017). However, one of the priorities for the future is to identify where the limits are in terms of the severity, spatial extent and frequency, beyond which forest ecosystems will no longer be able to compensate for their effects (Kulakowski *et al*. 2016). Altered disturbance regimes due to climate change and human pressure are currently having substantial negative impacts on forests and their biodiversity (Braunisch *et al*. 2014, Guz and Kulakowski 2020). The loss of natural regeneration ability (Rammer *et al*. 2021, Neary *et al*. 2022) and transformation into non-forest ecosystems (Millar and Stephenson 2015) in some forest types is a real possibility in the near future. It would, of course, entail major changes at the global level in the regulation of precipitation, carbon cycling, protection of soils from erosion, conservation of biodiversity, or provision of other ecosystem services on which humanity depends (Seidl *et al*. 2017).

In recent decades across Europe and North America, unprecedented disturbance activity has led to increased interest in forest dynamics by ecologists. Many questions have been raised regarding the causes of the widespread disturbances, the optimal way to treat them, and projections

for the future (Kulakowski *et al*. 2017). It has become of utmost importance to focus research efforts on primary forests - the last fragments of native forest cover that have not been directly affected by human activities to date. Historical disturbance regimes in beech- and spruce-dominated primary forests, which are the most widespread forest types in the Carpathian mountains, can be both described as mixed severity disturbance regimes, which means that disturbances of different severities and spatial extent are represented (Čada *et al*. 2020, Frankovič *et al*. 2021, Kameniar *et al*. in prep.). However, they differ to some extent due to the differences in tree species composition. The differences may also be partially attributed to the different levels of knowledge in these two forest types. The focus on spruce-dominated forests is a logical consequence of recent large-scale wind damage followed by insect outbreaks in natural spruce forests and, more importantly, in managed spruce plantations in lower elevations (Seidl *et al*. 2017, Hlásny *et al*. 2019). Nevertheless, there is also emerging evidence of large-scale synchronised disturbances in beech-dominated primary forests (Frankovič *et al*. 2021, Kameniar *et al*. in prep.).

The main disturbance factors in Carpathian spruce primary forests include windstorms and bark beetle outbreaks, mainly caused by spruce bark beetle (*Ips typographus*) and other related species (Čada *et al*. 2016, Holeksa *et al*. 2017, Kulakowski *et al*. 2017). Fire is not a regular disturbance agent, which differs from boreal spruce forests (Angelstam and Kuuluvainen 2004). In natural spruce forests, mixed-severity disturbance regimes have been described using dendrochronological and other methods in different areas: in the Bohemian forest, which is the mountain range close to our research area (Janda *et al*. 2014), but also in the Western (Janda *et al*. 2017), Eastern (Trotsiuk *et al*. 2014, Svoboda *et al*. 2014), and Southern Carpathians (Spînu *et al*. 2020). The most important results of this increased interest are that across large areas, synchronised disturbances are a natural part of the disturbance regime of montane spruce forests (Janda *et al*. 2014, Holeksa *et al*. 2017, Kulakowski *et al*. 2017), forests continue to regenerate spontaneously despite high severity and large-scale disturbances (Zeppenfeld *et al*. 2015), and that spruce forest biodiversity is well adapted, or even dependent on natural disturbances (Mikoláš *et al*. 2017b, Kozák *et al*. 2021, Kameniar *et al*. 2021, Ferenčík *et al*. 2022).

Despite common features, considerable variability in the disturbance regimes of the spruce forests of Central Europe has been reported. It is caused by factors such as slope orientation, relief ruggedness, soil type or humidity (Bałazy *et al*. 2019, Hlásny *et al*. 2021a, b). For example, not a single large-scale, high-intensity disturbance has been identified in a 200-year dendrochronological

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record from the northern side of the High Tatras and Babia Hora Mountain (Szczevczyk *et al.* 2011). In contrast, on the southern slopes, Holeksa *et al.* (2017) report up to 14 such disturbances based on historical and dendrochronological data. The frequency of wind calamities here has been increasing over the last 200 years, which can be attributed to the progression of spruce-oriented silviculture in the area. However, the most interesting fact is that disturbances caused by strong winds were not always necessarily followed by an overpopulation of bark beetles. Thus, today's bark beetle outbreaks may be a consequence of a warming and drying climate (Holeksa *et al.* 2017). The questions remain as to what extent the current disturbance regime in spruce montane forests is natural, and the exact influence of gradually increasing fragmentation of the native forest and changes in species composition of adjacent stands in favour of spruce has on bark beetle outbreaks. Indeed, these processes, together with the homogenisation of forest stands at the landscape level, reduce resilience to disturbances and also facilitate their spread (Franklin and Forman 1987, Peterson 2002, Hlásny *et al.* 2021). Despite these factors, the current large-scale disturbances in spruce-dominated primary forests in the Western Carpathians are still considered within the limits of the original disturbance regime, without any problems with regeneration (Janda *et al.* 2017).

In the last 250 years of disturbance history in the Western Carpathians, high and very high severity disturbances (over 40% of removed canopy cover) accounted only for 14.3% of all events. However, they were responsible for 42.3% of canopy removal (Janda *et al.* 2017). In contrast, low-severity disturbances were more common but removed only a small part of the canopy cover (Janda *et al.* 2017). Analysis by Čada *et al.* (2020), which focused more broadly on the spruce forests of the Carpathians, the Bohemian Forest in the Czech Republic, and the Harz Mountains in Germany, highlighted the role of moderate severity (25 – 70% of canopy removal) and moderate scale (patches larger than 10 ha comprised 58% of the total disturbed area) disturbances. Nevertheless, evidence of high severity and large-scale (up to 93 ha of 100% mortality) synchronised historical disturbance events was also found (Čada *et al.* 2020).

Although beech-dominated forests naturally cover much larger areas in temperate Europe than spruce forests, their disturbance regimes have been less well studied. This is likely because they tend not to experience such dramatic disturbances which negatively influence forestry management (e.g., Nagel *et al.* 2013, Nagel *et al.* 2016, Frankovič *et al.* 2021). However, recent studies show the situation may change soon, especially in beech stands that were planted or have simplified structures (Leuschner 2020). For example, high mortality rates were observed in beech

forests after a severe drought in southwestern Hungary (2000 – 2004), where approximately 120,000 m^3 of deadwood was salvage-logged (Lakatos and Molnar 2009). After the drought of 2018/2019, which affected large parts of Europe, many tree species, including beech and other broadleaved species, were heavily impacted (Brun *et al*. 2020).

In comparison with primary spruce forests, beech-dominated primary forest dynamics have typically been studied at smaller spatial scales using gap analysis and actual canopy cover (Drössler and von Lupke 2005, Orman and Dobrowolska 2017, Nagel *et al*. 2016, Feldmann *et al*. 2018) or historical measurements (Šebková *et al*. 2011, Drössler and von Lupke 2005). Only a few studies have used a dendrochronological approach to describe longer disturbance histories of beech-dominated primary forests (Šamonil *et al*. 2009, Nagel *et al*. 2014, Frankovič *et al*. 2021, Pettit *et al*. 2021, Kameniar *et al*. in prep.). There is still limited information about the frequency, severity and spatial extent of natural disturbances in primary beech forests and how they varied at the forest stand and landscape levels during recent centuries. Most of the studies highlight the role of gap dynamics - mortality of one or several trees (Splechtna *et al*. 2005, Šamonil *et al*. 2009, Orman and Dobrowolska 2017). In one study from the Slovakian Carpathians, 10% of canopy gaps were between 250 – 1,000 m^2 (Drössler and von Lupke 2005). The largest continual windthrow in the Carpathian beech-dominated primary forest was reported on an area of 8.3 ha (Feldmann *et al*. 2018). However, more recent dendrochronological studies, including our work, indicate significantly larger synchronisations of disturbances in this forest type (Frankovič *et al*. 2021, Kameniar *et al*. in prep.).

Disturbance dynamics can also be influenced to a great extent by species composition. Beech-dominated primary forests are much more heterogeneous than spruce-dominated. In our study (Kameniar *et al*. in prep.), in the spruce-dominated stands, spruce represented 87.1 – 99.2% of the basal area, with a median of 98.0%, while in the beech-dominated stands, the proportion of beech varied from 45.5 to 84.6%, median of 61.8%. Also, other studies report a high proportion of species other than beech - mainly spruce (30%) and fir (41%) of the total basal area (Parobeková *et al*. 2018, Frankovič *et al*. 2021). Synchronisations of disturbance peaks were found in valleys with higher dominance of beech (Kameniar *et al*. in prep.). In contrast, no major synchronisations of more severe disturbance peaks were found in the valley with the lowest proportion of beech, where half of the total basal area was represented by fir and spruce. Generally, mixed-species forests are more resistant to natural disturbances and environmental fluctuations than single-species

(Pretzsch *et al*. 2013, Jactel *et al*. 2017, Pardos *et al*. 2021). However, in the case of beech-dominated primary forests, spruce admixture can function as a destabilising element, especially when the beech-dominated forests are neighbouring subalpine spruce forests (Orman and Dobrowolska 2017). In such cases, bark beetles may spread from subalpine spruce forests to lower-elevation mixed forests and selectively kill spruce trees. Therefore, they can contribute to higher synchronisation of disturbance activity between both these two forest types and beech-dominated forests. We are witnessing a spruce decline in beech-dominated primary forests because of climate change (Parobeková *et al*. 2018).

Disturbances are processes that provide environmental heterogeneity at the habitat level (Pickett and White 1985) but also at the landscape level (Turner *et al*. 1994). Heterogeneity is closely linked to resilience - the ability of an ecosystem to absorb disturbance and undergo a state of change while maintaining its basic identity, functions, structures and responses (Walker *et al*. 2004). Higher heterogeneity (as well as the subsequent increased biodiversity) generally provides higher resilience (Walker 1995, Folke 2006). As mentioned above, disturbance is a key factor that promotes spatial heterogeneity and structural complexity of ecosystems (including forest ecosystems) and their biodiversity (Beudert *et al*. 2015). This implies that forest ecosystems shaped by natural dynamics (i.e. natural disturbances) are more resilient to disturbances - whether natural or anthropogenic - due to their higher biodiversity (on different levels), heterogeneity and diversity (Swanson *et al*. 2011). Conversely - ecosystems with long-term suppressed disturbances (and hence simplified structure) are much more vulnerable. There is also a known cumulative effect where suppressing less severe disturbances shifts the system too far away from natural variability (Turner 2010). A reversion back to natural limits can be catastrophic - a good example is the large-scale breakdown of spruce monocultures across Europe (Klimo *et al*. 2000, Schelhaas *et al*. 2003, Hlásny *et al*. 2021). These findings show that, in the context of climate change, it is essential to change the way forests are managed to best mimic natural disturbance regimes and thereby help increase resilience in the face of uncertain changes (Thompson *et al*. 2009, Lindenmayer *et al*. 2012, Braunisch *et al*. 2014). At the same time, there is still a need to ensure that as much of forests and other habitats are effectively protected as much as possible and are shaped solely by natural processes (Margules and Pressey 2000).

2.3 Influence of natural disturbances and forest structure on birds

Birds (Aves) are an ecologically important taxonomic group of forest organisms (Sekercioglu *et al*. 2004, Whelan *et al*. 2015), which have various demands on 3D forest structures for nesting, foraging and other activities (Brawn *et al*. 2001, Hanzelka and Reif 2016). Moreover, they are also easily observable, which makes them suitable as study objects in forest ecology. Birds are also important from a nature conservation point of view as an umbrella species (Mikoláš *et al*. 2019), flagship species (Kortmann *et al*. 2018) and indicator species (Braunisch *et al*. 2019).

As mentioned earlier, natural disturbances are natural processes in the forest ecosystem (Pickett and White 1985). The importance of disturbances in forest dynamics is indirectly confirmed by the fact that biodiversity, including bird communities, is often increased in early successional, recently disturbed areas (Drapeau 2000, Topercer *et al*. 2008, Klaus *et al*. 2010, Lewandowski *et al*. 2021). Species of later successional stages are typically also present, however, they are often at higher densities in areas not affected by disturbance (Topercer *et al*. 2000, Klaus *et al*. 2010). The importance of disturbances for birds is further confirmed, for example, by the study of Sauer *et al*. (2000), who analysed bird occurrence data from 1966 – 1998 across the North American continent. It was found that up to 40% of species that are in some way linked to disturbances experienced a significant decline in populations during this period. In contrast, a significant increase in numbers occurred in only 17% of species, probably due to management that eliminates or prevents the effects of disturbances (Litvaitis 1993).

Numerous studies worldwide have addressed the impact of disturbances on bird communities. Many have taken place in areas with a different disturbance regime than the Carpathian mountain spruce forests. In particular, papers from areas where fire is the primary disturbance factor are frequent (Azeria *et al*. 2011, Castro *et al*. 2010, Bock *et al*. 1978, Smucker *et al*. 2005). Although the disturbance regime is different in these areas, the mechanism of action is very similar - natural disturbances of varying magnitude and intensity promote ecosystem heterogeneity and hence increase the diversity of ornithocenoses (Smucker *et al*. 2005). As in our natural conditions, the "biological legacy" has a decisive influence - its removal during the salvage logging has a significantly negative impact on birds (Hutto and Gallo 2006).

In the Western Carpathians, many studies have been conducted in the past, focusing on birds in both mountain beech-fir-spruce (Korňan 1997, Korňan 1998, Saniga and Saniga 2004, Korňan 2004, Saniga 1995) and spruce-fir forests (Saniga 2009). However, these studies were not focussed strictly on primary forests and the effect of natural dynamics. Bird communities of beech- and spruce-dominated primary forests differ to some extent. However, generalistic species such as the common chaffinch (*Fringilla coelebs* Linnaeus, 1758), European robin (*Erithacus rubecula* (Linnaeus, 1758)) and others, which represent the majority of individuals, reach comparable abundances in both forest types (Saniga and Saniga 2004, Saniga 2009). Other species show a stronger or weaker preference for one of the forest types (Wesołowski *et al*. 2003; Tomiałojć and Wesołowski 2004), but only a minor group of species is strictly tied to one of them (Korňan 2004, Wesolowski *et al*. 2018, Kameniar *et al*. 2021). Typical species of spruce-dominated forests are, for example, the three-toed woodpecker (*Picoides tridactylus* (Linnaeus, 1758)), red crossbill (*Loxia curvirostra* Linnaeus, 1758)), Eurasian pygmy owl (*Glaucidium passerinum* (Linnaeus, 1758)) and the capercaillie (*Tetrao urogallus* Linnaeus, 1758) (Saniga *et al*. 2009, Kameniar *et al*. 2021). Beech-dominated forests are much more heterogeneous in terms of tree species composition than spruce-dominated (Parobeková *et al*. 2018, Frankovič *et al*. 2021, Kameniar *et al*. in prep.), therefore, it lacks typical species. However, when taking into account only spruce- and beech-dominated primary forests, there are species which occur almost exclusively in the latter one - the wood warbler (*Phylloscopus sibilatrix* (Bechstein, 1793)), collared flycatcher (*Ficedula albicollis* (Temminck 1815)), white-backed woodpecker (*Dendrocopos leucotos* Bechstein 1802) and the great tit (*Parus major* Linnaeus, 1758) are among them. However, these species also often occur in forest types below the beech-dominated belt. Various total numbers of bird species were reported from different Carpathian spruce-dominated primary forest and spruce natural forests localities: 38 from the Mt. Polica in Poland (Ślizowski 1991), 45 from the Great Fatra Mts. in Slovakia (Saniga *et al*. 2009) and 59 from the Slovak part of the High Tatra Mts. in Slovakia (Kocian *et al*. 2005). Bird communities are more diverse in beech-dominated primary forests: 48 species were reported from the Small Fatra Mts. in Slovakia (Korňan 2004) and 34 – 52 from the Great Fatra Mts., depending on the season (Saniga and Saniga 2004).

Norway spruce, silver fir and European beech are long-lived tree species - their lifespan reaches 400 – 500 years (Pavlin *et al*. 2021). Therefore, the cycle between two disturbances can also last a very long time. For this reason, it is almost impossible to investigate the long-term impact

of disturbance history on birds directly. Most studies deal either with the impact of human interventions (Mikoláš *et al*. 2017a), the short-term impact of a strong "stand replacing" disturbance or use the "space for time substitution" (Begehold *et al*. 2014, Baláž and Balážová 2012). Although the stand structure tells a lot about the history of disturbances, it cannot be determined with sufficient precision without dendrochronological data. Only a limited number of papers have included this kind of data in their analyses (see, e.g. Möning and Müller 2008). In the habitat of the Carpathian mountain temperate forests, only the studies by Mikoláš *et al*. (2017b) and Kameniar *et al*. (2021) used this approach.

Disturbances affect bird community composition primarily by influencing forest stand structure. At the habitat level, it is a major factor influencing birds (Cody 1985). Stand structure for birds is responsible for varying food availability, risk of predator attack, and nest site availability (Brawn *et al*. 2001, Hanzelka and Reif 2016). In general, the degree of structural heterogeneity of an ecosystem is correlated with the degree of biodiversity (Tews *et al*. 2004, Kebrle *et al*. 2022). Numerous studies showed that artificially simplified managed forests host only a certain proportion of original community diversity (Korňan 2006, Baláž and Kocian 2015), mainly more generalistic species with no special requirements on forest structure, for example, the common chaffinch or the European robin. Moreover, in simplified forests, even these generalistic species typically reach only lower abundances (Baláž and Balážová 2012). In general, this negative influence can be attributed to altering natural dynamics and the suppression of natural disturbances, which results in a scarcity of structural elements necessary for birds (Korňan 2006) and other parts of biodiversity (Mori and Kitagawa 2014).

Structural parameters typically differ significantly between formerly managed old-growth forests and primary forests, especially in vertical structure complexity, the number of trees with large DBH and the amount of dead wood (Commarmot *et al*. 2005). In managed and formerly managed beech-dominated forests in Germany, most of the breeding species (19 out of 37 analysed) were associated with the last third of the forest cycle, namely the terminal and disintegration phases (Begehold *et al*. 2014). The authors explain it by the presence of a large amount of dead wood, a higher number of trees of large size and also trees with microhabitats in these forest development phases. In contrast, no species preferred the late optimum developmental phase, and the preference for early and medium optimum was also low. The gaps were also not preferred by many species. These results are probably strongly affected by the effect of

management, although some of the plots were long without management. The research plots characterised as terminal and disintegration stages were the most similar to the primary forest, as they contained the highest amounts of structures resulting from natural mortality processes. Other stages differed much more from the natural state; for example, the gap was also the logged area in a managed forest. Even after a long time without management, they did not develop natural structures important for birds. However, in the primary forest, they are present in varying densities during the whole cycle (Parobeková *et al*. 2018), changing preference vs avoidance patterns in bird species.

Although biodiversity studies in managed and formerly managed forests are important, there is also the need to have reference data from unaltered or minimally altered forests shaped by natural dynamics. Along with this, it is crucial to be aware of shifting baseline syndrome, defined as "a gradual change in the accepted norms for the condition of the natural environment due to lack of past information or lack of experience of past conditions", which is a serious problem in ecological research (Soga and Gaston 2018). When human-simplified vegetation with altered dynamics and biodiversity is taken as a reference condition (e.g. Goodale *et al*. 2009), the impression is that further human influence is increasing biodiversity and improving it. Sometimes it can lead to the opinion that any attempts at strictly protected areas without forestry management are unjustified (Schulze *et al*. 2014). Such results can easily be misused to justify further exploitation (Luick *et al*. 2021a).

In the case of temperate mountain forests, only the protection of large areas with natural dynamics can safeguard the whole array of biodiversity, including the most sensitive species (Kozák *et al*. 2021, Ferenčík *et al*. 2022). At the same time, properly managed forests can also cover the needs of most organisms - up to 90% in Scandinavian spruce forests (Parviainen *et al*. 2000). It can be reached by retention of structural elements of natural forests in logged areas and designation of patches which are excluded permanently from logging operations (Kraus and Krumm 2013). In the case of deadwood, which is one of the crucial and also easily quantifiable forest structure elements, the thresholds required for the survival of the majority of saproxylic biodiversity were set for coniferous forests (20 – 30 m^3/ha) and for mixed montane forests (30 – 40 m^3/ha) (Müller and Bütler 2010). In the case of birds, especially some larger and more sensitive species, an important driver of their distribution is also the area of their habitat. The capercaillie was shown to prefer unfragmented forests with long distances to the closest road and settlements

(Mikoláš *et al*. 2016). For long-term survival, it needs $250 - 500$ km^2 of suitable habitat (Grimm and Storch 2000, Braunisch and Suchant 2013). Otherwise, the population gradually decreases. Another species requiring large areas of suitable habitat is the three-toed woodpecker - every pair requires 50 hectares of suitable habitat on average (Pechacek and d'Oleire-Oltmanns 2004). However, it was demonstrated that the occurrence of the majority of temperate forest birds is influenced by fragment size and distance to the forest edge (Hofmeister *et al*. 2017).

Currently, we can more often observe the impacts of disturbances in managed and previously managed forests than in protected primary forests. It is especially true for artificial spruce monocultures, which are rapidly deteriorating (Hlásny *et al*. 2021, Potterf *et al*. 2022). From an ecological point of view, it provides the opportunity to restore natural structure and associated biodiversity (Müller *et al*. 2008). In naturally regenerating windthrow and bark beetle outbreak areas in the High Tatra Mts. (Slovakia), 51 bird species were recorded $2 - 5$ years after the disturbance (Topercer 2000). In addition, up to 21.57% of them belonged to species of conservation importance, and no significant decline in the abundance of forest species was found (Topercer 2000). However, another study from formerly managed spruce forests in Šumava shows that the bird community's response also depends on the scale and severity of the disturbance (Kebrle *et al*. 2022). Small-scale high-severity or large-scale low-severity disturbances increase the heterogeneity of forest structure, which positively influences the bird species' diversity and abundance. The positive influence of small-scale gaps on the diversity of bird communities was also reported in beech-dominated natural forests (Kebrle *et al*. 2021). In contrast, severe and large-scale disturbances homogenise forest structure and decrease bird community diversity and abundance (Kebrle *et al*. 2022). It is essential to add that even severe and large-scale disturbance events in the Carpathian primary forests are not homogenising the structure in large continuous areas because of highly heterogeneous pre-disturbance structure, which is the result of past disturbance history (see chapter 2.2).

Although most mountain temperate forest bird species do not have very specific environmental requirements (Möning and Müller 2008), several structural parameters were identified as important for bird community diversity and abundance; tree species composition (Möning and Müller 2008), amount of coarse woody debris (Rosenvald *et al*. 2011) and its subtypes, especially standing dead trees (a key habitat for woodpeckers) (Costello *et al*. 2000, Pechacek and d'Oleire-Oltmanns 2004) and for species, which use them for hunting (Costello *et*

al. 2000). Further, uprooted trees are used by the Eurasian wren (*Troglodytes troglodytes* (Linnaeus, 1758)) and several other species for nesting (Saniga and Saniga 2004, Wojton and Pitucha 2020). Another important characteristics identified for forest birds include the presence of large habitat trees (Kebrle *et al*. 2021), overall age of forest stand (Poulsen 2002, Möning and Müller 2008), richness of vertical canopy structure (Goetz *et al*. 2007), degree of canopy openness (Möning and Müller 2008, Lewandowski *et al*. 2021), density of living trees (Mikoláš *et al*. 2017b), overall heterogeneity on stand level (Kebrle *et al*. 2022) and presence of various microhabitats (Piechnik *et al*. 2022), especially cavities, which are use by owls (Lõhmus 2003), stock dove (*Columba oenas* Linnaeus, 1758) (Murton and Isaacson 1962, Möning and Müller 2008) and collared flycatcher (Mitrus 2003). In fact, cavity-nesters represent a large proportion of the primary forest bird community - for example Saniga and Saniga (2004) reported that up to 43.1% of the total number of species recorded in a beech-dominated primary forest were cavity-nesters. All of these structural parameters in primary forests are directly created or influenced by natural disturbances. However, they are continuously changing across time and space and their actual values depend on the given disturbance agent (or their combinations), disturbance severity, spatial extent and timing (Kameniar *et al*. 2021, Mikoláš *et al*. 2017b). As the structure changes in time or space, different species are favoured. The common chaffinch, Eurasian nuthatch (*Sitta europaea* Linnaeus, 1758), song thrush (*Turdus philomelos* Brehm, 1831), goldcrest (*Regulus regulus* Linnaeus, 1758) and the common firecrest (*Regulus ignicapilla* (Temminck, 1820)) are more associated with mature forests. Conversely, species such as the common chiffchaff (*Phylloscopus collybita* (Vieillot, 1817)), willow warbler (Linnaeus, 1758)), three-toed woodpecker and the dunnock (*Prunella modularis* (Linnaeus, 1758)) benefit from more open spaces (Möning and Müller 2008, Begehold *et al*. 2014, Kameniar *et al*. 2021).

As described in the previous chapter, natural disturbance regimes are shifting due to climate change in recent decades; disturbances are becoming larger, more frequent and more severe (Seidl *et al*. 2017, Hlásny *et al*. 2021). In Central Europe, these changes are mainly reported from managed forests, which are more susceptible to disturbances (Thompson *et al*. 2009, Potterf *et al*. 2022). Mortality in beech- and spruce-dominated primary forests is still within the variability of the last centuries (Synek *et al*. 2020, Frankovič *et al*. 2021). Therefore, it can be argued that climate change has had some indirect positive influences on birds in some beech and spruce dominated forests as the size of areas under strict protection is increasing (see chapter 7), and in large areas of

simplified managed forests, natural dynamics are more frequently allowed. Thus, the structure is becoming more heterogeneous and more suitable for the native bird community (Topercer 2009). However, along with the positives, there are also negative impacts of climate change on birds. Firstly, the homogenisation of forest landscapes as a result of climate-induced large-scale and high-severity disturbances can decrease the overall diversity of the bird community in altered forests (Kebrle *et al*. 2022). Secondly, climate-related habitat shifting can cause the contraction of some mountain biotopes. In the context of Central European forests, it is mainly the case of spruce-dominated primary forests. These forests with their associated biodiversity mostly occupy only the uppermost parts of mountains. Therefore, they cannot shift to upper elevations and their local populations are at risk of extinction (Braunisch *et al*. 2014).

2.4 Impact of anthropogenic disturbances on birds

Human interventions (anthropogenic disturbances) in the natural environment always alter it in some way and disturb its natural functioning. Due to the interconnectedness and complexity of their relationships, the consequences of these interventions often have a cascading effect and are negatively manifested at both regional and global scales (Chapin *et al*. 2000). In the Carpathians, they have been human interventions in the native forest very pronounced for a long time - forests at lower elevations have been destroyed or significantly altered already in historical times. Mountain spruce forests were also extensively burnt and cut down for sheep grazing during the Wallachian colonisation (from about the second half of the fourteenth century) in many places (Mikoláš *et al*. 2021). Nevertheless, due to their relative inaccessibility, some parts of them have been preserved in an almost intact state (apart from grazing and scattered selective logging in the vicinity of the alpine meadows). In recent decades, however, even these last remnants of native forest have been accessed and used for industrial timber production (Mikoláš *et al*. 2017a). In most of the area, the native forest has been completely replaced by a different, simplified stands that does not meet the requirements of many native species (Knorn *et al*. 2012).

Anthropogenic disturbances in forests can vary in nature and effect. In our conditions, more serious encroachment on the forest invariably causes major, sometimes irreparable, damage. The last remnants of forests that have been continuously shaped by natural processes and not by human activity are disturbed or completely removed (Knorn *et al*. 2012). We are thus losing the last refugia of native forest biodiversity, hydrological and climatic regulatory systems, as well as hitherto

unappreciated opportunities for scientific research, non-invasive tourism and recreation (Shin *et al*. 2010).

There is a large body of literature that addresses the impact of human activities on bird communities in forest environments. Mentioning this part of the issue is very important given that the aim of this work is to shift perceptions of forest management towards more sustainable models that take greater account of the non-productive functions of forests, including biodiversity conservation, in addition to their productive functions. It is also necessary to clarify to the public and forest users/managers the differences between natural and anthropogenic disturbances.

Logging and other activities carried out during forest management are the most important anthropogenic disturbances affecting bird population dynamics (Virkkala 2004). The impact on birds is mainly due to changes in tree species composition and vegetation structure (Willson 1974). When assessing the impact of different management practices on ornithocenoses, it is very important to distinguish whether the anthropogenic disturbance is occurring in a habitat previously altered by humans, or whether it is an intervention in the original environment. Neglecting this important aspect may lead to erroneous conclusions about the general benefits of certain types of management interventions for bird communities (Goodale *et al*. 2009, King and DeGraaf 2000). For example, the above-mentioned authors concluded that some small-scale forest management interventions increase bird biodiversity. However, they used as a reference native condition in the first case an adult unmanaged forest that had been established on a former pasture about 150 years ago (Goodale *et al*. 2009), and in the second case an adult unmanaged forest with a closed canopy with no visible recent signs of management activities (King and DeGraaf 2000). Thus, in both these cases, a simplified unnatural, human-significantly influenced stand in which disturbance of the monotonic structure may have actually increased diversity served as a reference condition. Studies assessing the impact of human activity on forest ornithocenoses should always keep in mind a condition as similar to the original one as possible, with as little human influence as possible. This goal can only be met by conducting research in forests that have been minimally altered by humans (Gilg 2005). For example, Baláž and Balážová (2012) in their work divided the studied sites in the Western Carpathians into 3 groups - natural spruce forest of the upper forest limit, natural mixed forest and artificial spruce monoculture, where the highest areas were those with natural spruce forest and the other two types had approximately the same, significantly lower altitude - around 1000 m above sea level. In this case, spruce forest was the best-preserved type of environment. An

interesting result was that the richest ornithocenoses were found there. Despite the fact that, in general, the number of species in most taxonomic groups, including birds, decreases with altitude (Kocian 1998, McCain and Grytnes 2010). Thus, this means that species diversity is more strongly determined by the naturalness of the forest than by altitude. Baláž and Kocian (2015) came to the identical finding. Baláž and Balážová (2012) add that nine species were found in the unmanaged mixed forest that were not found in human-influenced habitats, of which six species were of European importance. In contrast, no other species were found in the area located in the middle of the spruce plantation than in the area located in the primary forest and in the forest, little altered by humans.

In general, it is important to be as comprehensive as possible in terms of the number of taxonomic groups (and processes) involved when assessing the impact of human interventions on biodiversity, as improving conditions for one small group of species may not be sufficient to justify an intervention that will negatively affect a much larger number of species or processes. Thus, the broader landscape or global ecosystem level contexts, which include influences on ecosystem services, resilience to climate change, etc., must also be considered (Millennium Ecosystem Assessment 2005, Donaldson *et al*. 2017).

2.4.1 Fragmentation and habitat loss

The indirect negative impact of humans on bird communities arises primarily through alteration of their environment - its structure and extent. In principle, these impacts could be summarised into two categories - 1. habitat loss/significant habitat alteration, 2. increased habitat fragmentation (Fahring 2003). Areas that were not directly altered were often significantly fragmented. As a result of fragmentation, bird species that were not naturally present can start to use the forests and paradoxically enrich the ornithocenoses (Fahring 2003). On the other hand, however, several native species that require large areas of more significantly undisturbed forests have been displaced (Goodale *et al*. 2009). A good example of a species tied to large forest complexes, shaped predominantly by natural dynamics, is the capercaillie (Mikoláš *et al*. 2017b). For a long-term sustainable population (470 – 500 interacting individuals), it needs 250 – 500 km^2 of sufficiently connected suitable habitat (Grimm and Storch 2000, Braunisch and Suchant 2013). Another species that is relatively space-demanding and thus sensitive to habitat loss and fragmentation is the three-toed woodpecker. This woodpecker is associated with natural mountain

spruce forests and requires a minimum of 60 ha of optimal habitat for each breeding pair (Pechacek and D'Oleire-Oltmanns 2004). Thus, large, unfragmented areas with a natural forest structure are required for its conservation.

Habitat fragmentation has many other negative impacts (Fahrig 2003). These include, for example, increased parasitism and predation on songbird nests due to edge effects as a consequence of logging (Weinberg and Roth 1998, Ford *et al*. 2001), or, in some species, impaired conditions for the development of juveniles, manifested by their lower weight (and thus lower viability (Huhta *et al*. 1999). Thus, in general, human-induced fragmentation can be said to have rather negative impacts on forest ornithocenoses (Wiens 1994, Keyser *et al*. 1998, Weinberg and Roth 1998, Ford *et al*. 2001).

Biodiversity of bird communities is higher in large complexes undisturbed by humans, even after taking into account non-native species that "enrich" the human-fragmented remnants (Saniga 1995, Bashta 2007, Bončina 2000). This is due both to the aforementioned demand of some species for habitat area, but also to the higher structural complexity of the forest, which is reduced by management treatments. Human impact is leading to the loss of structural elements to which several specialised species or entire ecological guilds are linked - in spruce forests, for example, cavity nesters (Saniga and Saniga 2004).

2.4.2 Impact of different management types

Although forest management will understandably always have some impact on biodiversity, this impact is not the same for every management practice. Korňan (2006) lists four basic management practices and summarises their impact on bird communities: 1. clearcut and 2. shelterwood, which can be both collectively described as even-aged, and 3. Single-tree selection and 4. group selection (uneven-aged management practices). All of these management methods eliminate structural elements in the forest stand that are irreplaceable for birds and other organisms, such as different types of cavities, crevices, dying or deformed trees, and deadwood in various stages of decomposition (Mollet *et al*. 2013). These elements are often associated precisely with trees that have exceeded the length of the rotation period. There is no shortage of such trees in a natural forest regulated by natural processes, but none of the common management practices take their importance sufficiently into account (Mori and Kitagawa 2014).

Clearly, the most serious negative impacts on biodiversity in general are those of the same-aged methods, most notably clearcut management (Korňan 2006). In contrast to natural disturbances, the aforementioned "biological legacy" does not remain in place in this case (Lindenmayer and Franklin 2002, Seidl *et al*. 2014). Most of the biomass is removed, the soil cover is disturbed, and long-term stable (or continuously changing) environmental factors such as daily and annual temperature amplitude (Petrík *et al*. 1986), soil moisture (Mařan and Káš 1948), and air humidity (Pobědinskij and Krečner 1984) change dramatically. This method of management is still commonly used even in Carpathian protected areas, despite the fact that its negative effects on the landscape as a whole have long been known and its use in high mountains is explicitly inappropriate due to the natural conditions (Keenan and Kimmins 1993).

The long-term consequence of clearcutting is the creation of structurally and age homogeneous multi-hectare units that have no counterpart in natural forests. Such forests are mostly only favourable for generalists or species tied to early successional stages (Thompson *et al*. 1992). In particular, spruce monocultures lack species tied to the shrub understory; Thompson (1992), based on a published model, predicts that under a clearcut management with a 100-year rotation period, there may be up to a 40 percent decline in the populations of interior bird species that prefer old-growth forest stands. According to the author, the decline occurs mainly as a result of conversion of old forest units into management forests, which results in degradation of habitat quality.

Similar deviation from the natural state occurs with so-called salvage logging, which is often practiced in protected areas where nature conservation is declared as the most important goal (Thorn *et al*. 2014, Mikoláš *et al*. 2017a, Spînu *et al*. 2020). This phenomenon is particularly relevant in recent decades, when, especially in the Northern Hemisphere, the extent and intensity of disturbances have increased rapidly (Seidl *et al*. 2014, Seidl *et al*. 2017) and serious clashes of interests between owners, forest managers and conservationists are emerging (Lindenmayer *et al*. 2017). Salvage logging in Carpathians is often not spatially limited by law, thus calamitous timber is processed on areas orders of magnitude larger than in normal planned logging. This results in homogenisation of the environment on areas of up to hundreds or thousands of hectares (Michalová *et al*. 2017). In addition, as a result of the removal of most of the biological heritage, the successional trajectory of the affected area changes completely - there is a shift in the species composition of vegetation from late successional species to pioneer species, in the conditions of

the spruce forests of the High Tatras mainly to grasses (Michalová *et al*. 2017). Changes in vegetation cover and its development are also reflected in the composition of communities of other organisms. Thorn *et al*. (2017) published a global meta-analysis that showed that salvage logging had a significant effect on eight out of the 24 taxonomic groups studied, with saproxylic organisms obviously being the most affected. Among birds, it primarily affects cavity nesters, which use dead standing trees for nesting in natural conditions (Thorn *et al*. 2017, Hutto and Gallo 2006).

Thorn *et al*. (2016), comparing treated and untreated naturally disturbed area, came to a seemingly different conclusion - the disturbance itself had a greater impact on bird communities than the subsequent salvage logging. However, they point out, this result is highly dependent on the nature of the disturbance - in the case of the Bavarian Forest, it was a severe disturbance that reduced tree cover by up to 90%. This meant that not many standing live and dead trees remained on the affected site, to which a whole guild of cavity-nesting birds (woodpeckers, owls, but also many songbirds) are attached. In the case of disturbance, where such structures naturally remain on the disturbed area, subsequent salvage logging has a far more pronounced effect on bird communities (Hobson and Schieck 1999).

3 Aims and overview of the dissertation thesis

Understanding natural dynamics, forest structure, biodiversity and relationships among them in unmanaged primary forests is inevitable for conservation and sustainable forest management in the age of ongoing biodiversity and climate crisis. Our thesis, based on data from more than 300 research plots in mountain beech- and spruce-dominated primary forests in Western and Southern Carpathians, aims to advance the state of knowledge in between-forest types synchronisation of natural disturbances and their impact on forest structure and biodiversity. In particular, the thesis aims to explore the synchronisation of disturbance events between beech- and spruce-dominated forest stands and the effect of disturbances and forest structure on bird assemblages. Birds were selected as a model taxonomic group because they are organisms sensitive to forest structure and able to shape it to some extent. At the same time, they are helpful in practical nature conservation as an umbrella, indicator and flagship species. Beech- and spruce-dominated forests are forest types of major importance in temperate Europe. Studying them in their primary state is important for forest management to shift towards close-to-nature forestry. Understanding the variability of disturbances, structure and biodiversity in primary forests can help us to evaluate current and future changes, resulting from climate change.

Particular aims of the thesis are to:

1. Describe the historical disturbance regime with the focus on disturbance synchronisation, in primary forest landscape, which is containing beech and spruce forest type (Section 5.1).

2. Investigate the influence of historical disturbances in spruce-dominated primary forests on forest structure and bird assemblages (Section 5.2).

3. To compare forest structure and bird assemblages' composition in beech- and spruce-dominated primary forests (Section 5.3).

4 Methods

4.1 Synchronised disturbances in spruce- and beech-dominated forests across the largest primary mountain forest landscape in temperate Europe

4.1.1. Study area

We conducted our research in the Făgăraș Mountains, located in the South Carpathian Mountains of Romania. Although primary forest logging has accelerated in the Făgăraș Mountains recently, and much of the area is not protected (Luick *et al*. 2021a), the inaccessible primary and old-growth forests still cover around 27,000 – 61,846 ha of the forested area (Schickhofer and Schwarz 2019). The Făgăraș Mountains represent the most completely preserved complex mountain forest ecosystem both in the Carpathians and likely in the wider zone of temperate Europe (Schickhofer and Schwarz 2019). The region is ideal for investigating natural disturbance processes over large spatial scales and altitudinal gradients.

Primary spruce- and beech-dominated forests, the focus of our study, occur on slopes between about 900 and 1,700 m in elevation (Popa and Kern 2009; Cenuşă 2010). In the spruce forest (1200 – 1700 m), *P. abies* is the dominant tree species, with a lesser admixture of *Sorbus aucuparia* L., and rarely *Pinus cembra* L., *Larix decidua* Mill., *Acer pseudoplatanus* L., and *Betula pendula* Roth. The average annual temperature in the spruce stands is 3.5 °C, with an average temperature of 9.5 °C during the growing season (Fick and Hijmans 2017). Beech-dominated forests are located in the lower parts of valleys, up to elevations around 1,400 m. Above 900 m elevation, beech is mixed predominantly with *Abies alba* Mill. and *P. abies*; *A. pseudoplatanus* and several other species are present only rarely. The average annual temperature is 5.2 °C, with an average temperature of 11.5 °C during the growing season.

4.1.2 Study site selection

We characterised our study areas as 'primary forests' because they are stands that have developed under a regime of natural disturbances and show little to no evidence of past human

impact. However, all stands are not necessarily in an old-growth stage of development, and many stands are post-disturbance, early-successive forest patches resulting from recent natural disturbances. Potential study sites were first selected using a previous inventory of primary forest remnants in Romania (Veen *et al.* 2010). These stands were then located in the field and surveyed for indicators of naturalness (e.g. coarse woody debris in various stages of decay, pit and mound topography) and signs of human impact; stands with evidence of past logging and grazing were avoided, as were stands close to formerly grazed areas. Additionally, we searched the available information from local archives regarding the history of land use in these areas to supplement our surveys. Historical data indicated that the areas selected for the study were not logged in the eighteenth and nineteenth centuries and have been protected since that period. Structural parameters at the stand level indicate high measures of naturalness in sampled stands (Tab. A1, Tab. A2).

4.1.3 Data sampling

We selected 11 valleys throughout the Făgăraș Mountains (Fig. 1). Nine valleys are located along the north face and two along the south face of the east-west oriented mountain range. Between 2011 and 2015, we established 191 plots in 15 stands (10 spruce- and 5 beech-dominated) with an average of 12 plots per spruce- and 14 plots per beech-dominated stand. In four valleys, the research plots were located in both spruce- and beech-dominated stands.
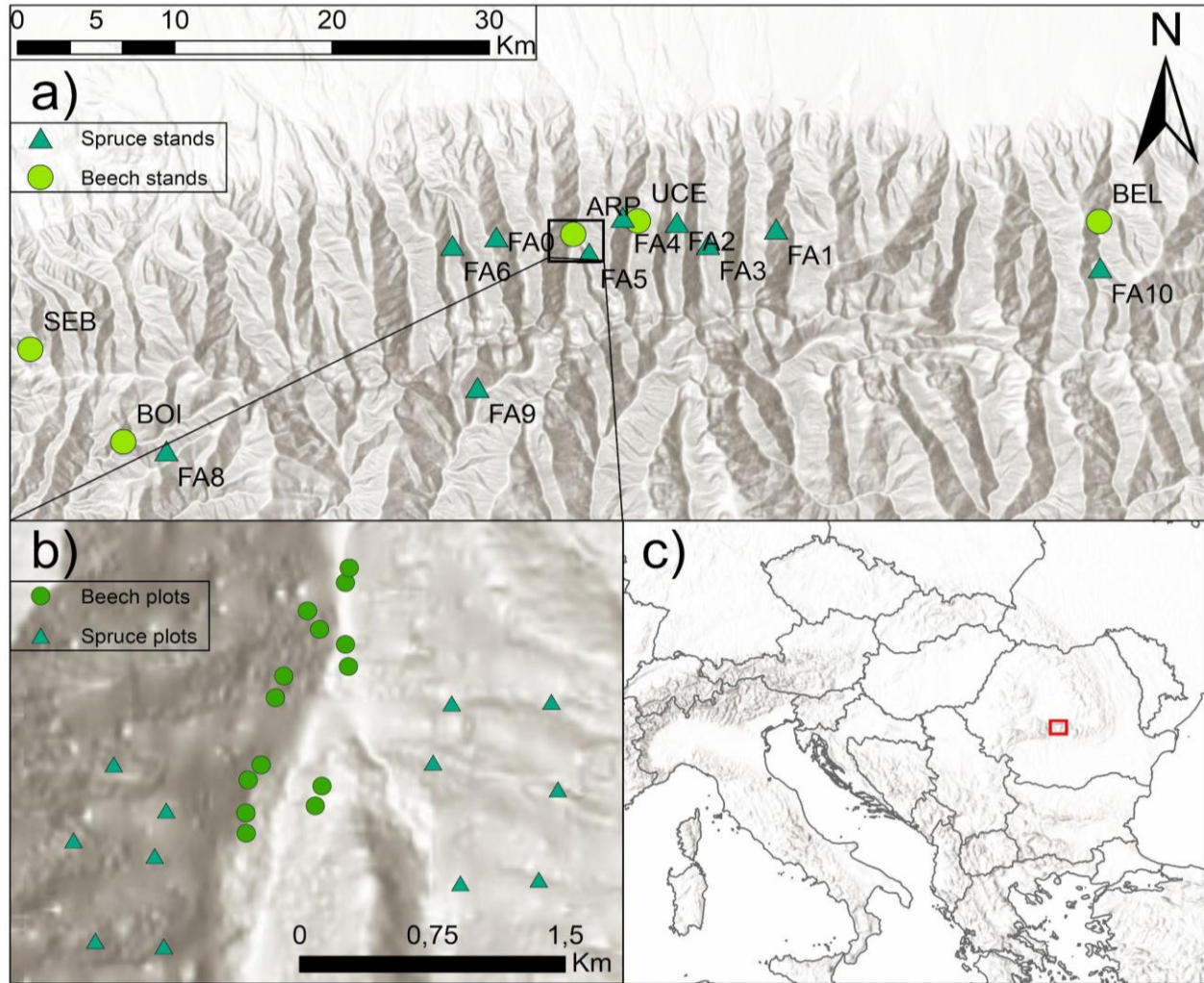
Fig. 1 Spatial distribution of study sites: a) location of beech- and spruce-dominated stands in the Făgăraș Mountains; b) example of plot distribution within one stand (Arpaselu); c) location of Făgăraș Mountains, Romania within Europe.

To position plot centres, a square grid was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011) for each stand, and plot centres were placed using a stratified random design (Schurman *et al*. 2018, Frankovič *et al*. 2021). Within the inner part of each cell, three random points were generated. If the first point was unsuitable (e.g., rocks, water, steepness), then a second (or rarely third) randomly generated point was used. In beech-dominated stands, we positioned a pair of circular plots (radius of 17.84 m) along the contour, one on each side of the identified random point. Paired plot centres were 40 m from the random point and 80 m from each other. Spruce plots were established directly on randomly generated points with a radius of 17.84 or 12.62 m, depending on the stand density.

For each plot, we recorded the GPS position and tallied all living trees with a diameter at breast height (DBH) of 10 cm or greater, as well as its species, DBH, and current canopy status (released - trees with crowns receiving at least 50% of direct sunlight; suppressed - trees with crowns receiving mostly diffuse sunlight). The diameter of horizontal crown projection was measured with an ultrasound device for a sample of trees to establish statistical relationships between crown area and DBH, which was later used to estimate the proportion of disturbed canopy area. Electronic and laser measuring devices linked to a GIS (Field–Map, IFER) were used to map the positions of all trees within plots.

For disturbance history reconstruction and age estimation, increment cores were extracted from living trees at 1 m height from the base, perpendicular to the slope direction. In spruce plots, 15 or 25 (depending on the plot radius, 12.62 or 17.84 m) randomly selected trees with DBH ≥ 10 cm and canopy status classified as currently released were sampled. If there were not enough trees on the plot, the closest trees outside the plot were selected, and rotten trees were replaced by a nearby tree with similar DBH to obtain the required sample size. An additional five randomly selected suppressed trees were cored to establish a growth-rate threshold for open canopy recruitment. In mixed beech-dominated plots, a subplot with a radius of 7.99 m was established around the centre, where all trees (released and suppressed) with DBH ≥ 10 cm were sampled. On the remaining part of the plot all released trees with DBH ≥ 10 cm and all suppressed trees with DBH ≥ 15 cm were cored, in addition to three randomly selected suppressed trees with DBH between 10 and 15 cm. Further, 12 regularly distributed points were established outside the plot within a radius of 25.23 m from the plot centre, and at each point the closest released tree with DBH ≥ 10 cm was sampled. Six of the 70 beech plots followed a slightly different design where on the remaining part of the plot all trees (released and suppressed) with DBH ≥ 20 cm plus 25% of released trees with DBH between 10 and 20 cm were randomly selected and cored, and all trees (released and suppressed) with DBH ≥ 60 cm were sampled outside the plot within a radius of 21.85 m from the plot centre. The study plots were established as a part of the REMOTE Primary Forests network (www.remoteforests.org) and the differences in sampling design are due to the evolving needs of this long-term project. For the purpose of this study, we account for the different sampling intensity by standardising prior to the disturbance history reconstruction (for details, see section 4.1.5).

4.1.4 Increment cores processing

Cores were processed using standard dendrochronological techniques and ring-width series were measured with a stereomicroscope using a LINTAB sliding table and TsapWin software (RINNTECH, Heidelberg, Germany, http://www.rinntech.com). Crossdating was performed according to the marker years approach (Yamaguchi 1991) and verified with PAST4 (www.sciem.com), CDendro (Holmes 1983, Larsson 2003), and COFECHA (Holmes 1983) softwares. For core samples that missed the pith, the number of missing rings was estimated using the method of Duncan (1989). The total number of processed cores was 6,479 (3,206 from beech-dominated forests, 3,273 from spruce-dominated forests); cores that could not be properly crossdated (rotten, damaged) were excluded from further analysis, resulting in 5,474 valid core samples (2,447 from beech- and 3,027 from spruce-dominated forests).

In the next step, radial growth patterns were analysed to identify two types of tree canopy accession events: (1) release – abrupt, sustained increase in tree growth, indicating mortality of a former canopy tree, and (2) open canopy recruitment – rapid juvenile growth rates indicating recruitment in a former canopy gap (Lorimer and Frelich 1989). Releases from suppression were identified by the absolute increase method (Fraver and White 2005) as pulses where the difference between average growth rates of adjacent 10-year running intervals (absolute increase) was greater than or equal to 1.25 standard deviations of all the calculated absolute increase values. To avoid false detection when mean growth rates are largely influenced by several extreme years, increases had to be sustained for at least seven years to be considered a release event (Fraver *et al*. 2009). To minimise the overestimation of disturbance severity caused by lateral releases of mature trees already present in the canopy (Lorimer and Frelich 1989), an optimal cutpoint (DBH = 26.9 cm) separating the subcanopy and canopy trees was estimated using DBH distribution of suppressed and released trees (Fig. A1). Release events detected when the tree DBH was above or equal to this threshold were then excluded from the disturbance history reconstruction. For the detection of open canopy recruitment, early growth rates of released and suppressed trees were calculated as 10-year averages from age 5 to 14 years (Lorimer and Frelich 1989, Splechtna *et al.* 2005) and used to estimate the optimal cutpoint separating trees originated in the open canopy from those found under closed canopy conditions (Fig. A2). Trees with an early growth rate greater than or equal to the established threshold were considered recruited under open canopy conditions. Because shade-tolerant tree species may need more than one disturbance to reach the canopy (Lorimer and Frelich

1989), multiple canopy accession events were allowed for individual trees in both spruce- and beech-dominated stands.

4.1.5 Disturbance history reconstruction

The percentage of disturbed canopy area at the plot level was calculated for each year as a sum of the current crown areas of reacting trees (showing release or open canopy recruitment) divided by the total crown area of all the sampled trees. Current crown areas were predicted based on a trees' current DBH using two linear mixed-effects models for coniferous (n = 814, R^2 (marg.) = 0.577, RMSE = 0.881 m) and broadleaved (n = 449, R^2 (marg.) = 0.657, RMSE = 1.590 m) species, with random intercepts accounting for the sampling design levels (stand, plot). The models were calibrated on the measured subsample of trees (for details see section 4.1.3). To correct for differences in core sampling intensity, only currently released trees within the 17.84 m radius from the plot centre and replacements for missing or rotten trees collected in spruce stands were used for disturbance history reconstruction. Additionally, each plot was resampled by randomly taking 1,000 subsamples of size m = 12 (the maximum common number of available tree records per plot). The calculation of the disturbed canopy area percentage was performed for each subsample separately and then averaged on an annual basis to produce the final plot-level chronology. The reconstructed disturbance chronologies were limited to 300 years (1700 – 2000) to avoid potential bias due to the small number of sampled trees originating before this period. To improve the temporal accuracy of the disturbance history reconstruction, a kernel density function was fitted to each annually binned chronology of disturbed canopy area percentage (Trotsiuk *et al.* 2018).

4.1.6 Spatiotemporal synchrony of disturbance dynamics

We explored the synchrony of natural dynamics by quantifying congruent patterns in disturbance time series. The overall synchrony of time series dynamics was quantified using Kendall's coefficient of concordance – W (Kendall 1970). The coefficient ranges from 0 to 1 and measures the level of agreement between two or more ranked time series. The maximum value is achieved when the rankings in each series agree perfectly over the years, while the minimum value signifies a lack of synchrony. This approach to analysing synchronicity assesses not only disturbance, but also an opposite process of regenerating canopy cover, as well as the pace of both of these changes with annual resolution. We quantified overall synchrony at two hierarchical spatial

scales. At the stand level, Kendall's W was calculated using plot-level time series within each stand while keeping data from different forest types separated. At the landscape level, we calculated the synchrony within beech-dominated forests and spruce forests using the plot-level time series across the whole sampling area. However, because Kendall's W depends on the number of time series involved in the calculation (Gouhier and Guichard 2014), we cannot directly compare levels of synchrony across stands or forest types differing in the number of time series (11 – 14 plots per stand; 70 and 121 plots in beech-dominated and spruce forests, respectively). To facilitate the comparisons, we resampled the original pool of time series and calculated the coefficients of concordance as mean values over 10,000 randomly taken subsamples of size m = 10. The procedure is equivalent to m-out-of-n bootstrap and allows us to estimate the confidence intervals (Bickel and Sakov 2008).

Regression analysis was employed to assess the differences in stand-level synchrony between beech-dominated and spruce forests. Because the values of Kendall's W are bounded between 0 and 1, we used the model assuming a beta probability distribution of the response (Ferrari and Cribari-Neto 2004). The flexible beta regression model defined by mean and precision (inverse dispersion) parameters enabled us to accommodate for non-constant variances between the forest types (Cribari-Neto and Zeileis 2010). Thus, we modelled both mean stand-level synchrony and its variance as functions of forest type. Allowing for heterogeneous variances between forest types considerably improved the simpler model assuming constant variances (ΔAIC = 46.5). We inversely weighted the values of concordance coefficients by their associated standard deviations to account for the differing precision of their estimates (i.e., less weight was given to estimates with higher uncertainty). The statistical significance of the model parameters was evaluated using partial Wald tests (Cribari-Neto and Zeileis 2010).

We further explored similarity in the disturbance synchrony within and between forest types using distance-based redundancy analysis – db-RDA (Legendre and Anderson 1999). First, we calculated the matrix of pairwise concordance coefficients among the plots. The matrix was converted to dissimilarities by subtracting W values from unity; perfectly synchronous pairs of plots have pairwise dissimilarities of zero while those with a total lack of synchrony have one. The dissimilarities were subsequently transformed into eigenvectors in principal coordinate analysis and submitted to the RDA. Since the sampling plots were spatially nested within stands, we employed partial db-RDA and partialled-out the effect of stands prior to the test for differences in

synchrony between the forest types (randomization test with 10,000 permutations). The analyses were performed in R (R Core Team 2021) using the libraries betareg (Cribari-Neto and Zeileis 2010), ggplot2 (Wickham 2016), synchrony (Gouhier and Guichard 2014) and vegan (Oksanen *et al.* 2020).

4.2 Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition

4.2.1 Study area

Our study was conducted in the Western Carpathian Mountains, Slovakia, between 48°63' and 49°52'N and between 19°30' and 20°12' E. We focused on ten forest stands between 1,244 and 1,534 m located inside primary forest remnants recognized by the national inventory of primary forests in Slovakia (Jasík and Polák 2011, Mikoláš *et al*. 2019).

Focal study stands were distributed in five mountain ranges with the largest areas of primary spruce dominated forest – the Tatra Mts. (four stands), the Low Tatra Mts. (two stands), the Great Fatra Mts. (two stands), the Orava Beskids (a single stand) and the Poľana Mts. (a single stand). Most of the stands were located on intrusive and metamorphic, acidic bedrock. Location of stands is displayed in the Fig. 2. Size of the study sites (primary forest fragments) varied from 41 to 494 ha, 185.4 ha on average. They are surrounded mostly by forest of differing naturalness: mixed primary forests, other natural forests, production forests). Some parts are bordering with salvage-logged areas and alpine habitats. However, these environmental variables were not taken into account. Tree species composition in the study area was strongly dominated by Norway spruce (over 90%). Other species, such as rowan (*Sorbus aucuparia* L.), fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.), larch (*Larix decidua* Mill.), pine (*Pinus* spp.), and birches (*Betula* spp.), were present only as an admixture (Janda *et al*. 2017). Area of primary forest stands varied from 41 to 494 ha (mean 185.4 ha). Annual mean temperatures range from 1.6 to 3.4 °C. Annual precipitation varies from 1,205 to 1,365 mm yr^{-1}, with more humid stands in the Tatra Mts. (Kozák *et al*. 2021).

In the above mentioned 10 stands, 145 plots were established as a part of an international primary forest research project (www.remoteforests.org), using a stratified-random design (Svoboda *et al*. 2014). Dendrochronological disturbance history data were previously published in Janda *et al*. (2017). For bird assemblage sampling, we selected 58 selected plots (six plots per stand with the exception of one stand in the Tatra Mts. containing only four plots). In each stand, study plots were selected to cover the whole gradient of disturbance severities and timing over the last 250 years. For this purpose, we split plots from Janda *et al*. (2017) according to disturbance event timing into three equally large classes.
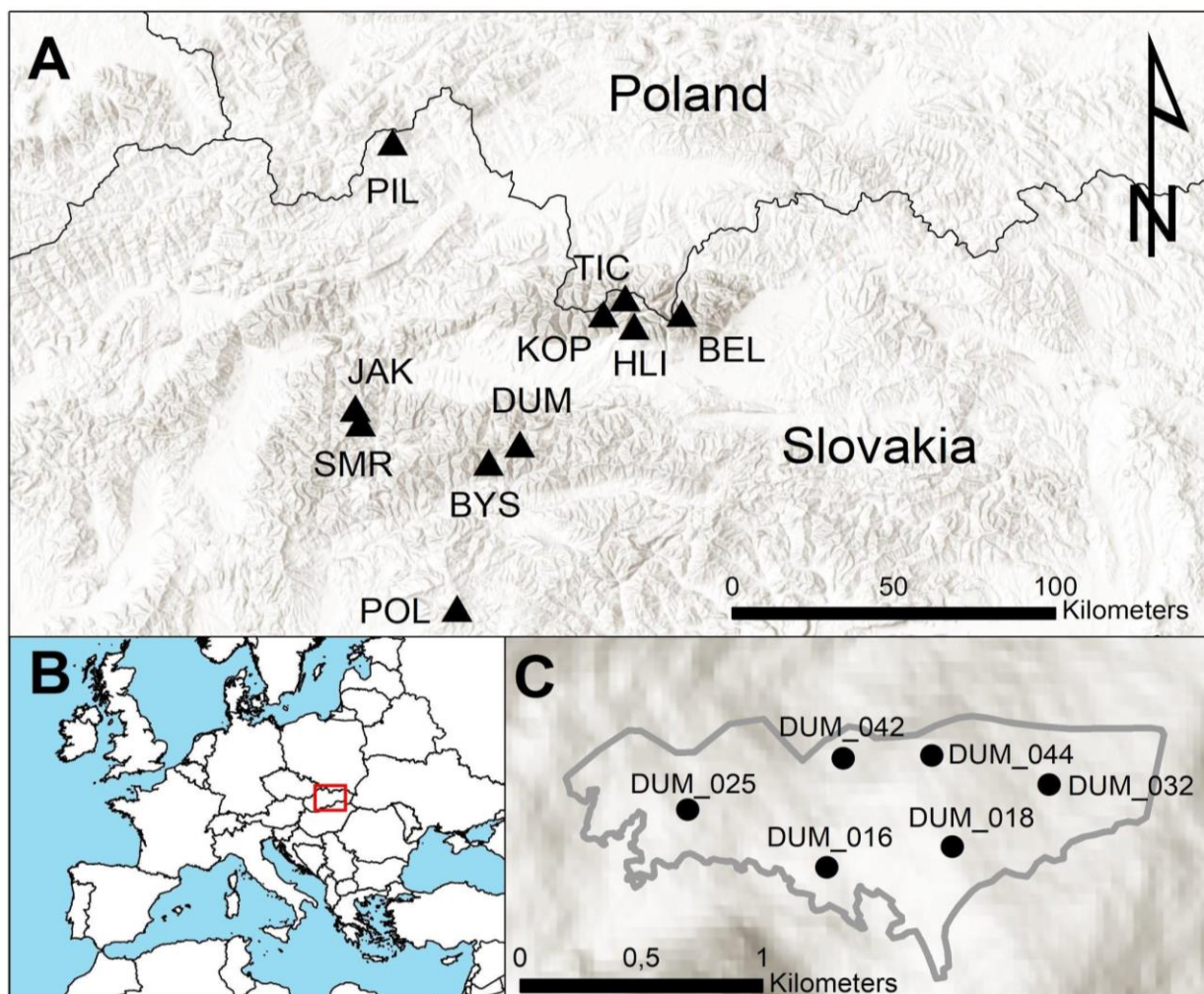
Fig. 2 a) research stands location in Western Carpathians, b) location of Western Carpathians in Europe, c) example of research stand.

We then selected two plots within each class on every stand, with differing severity if available. At the same time, we avoided locating any additional plots within 150 m around a given plot to minimize multiple counts of individual birds at different plots. Average distance among plots within the stands was 1.2 km (range 0.5 – 2.8 km).

4.2.2 Forest structure data

Forest structural parameters were measured in 2017 in all study plots within a circular area of 1,000 m^2 (17.84 m radius from the plot's centre) in the Poľana Mts. and 1,500 m^2 (21.85 m) in all other stands. Plots in Poľana were established according to a slightly different, albeit comparable protocol. To account for this difference, in the analyses all parameters were standardized per ha. Centres of the plots were then used as bird counting points. Number of regenerating trees was counted on the plot-level in three height categories: 0.5 – 1.3 m; 1.3 – 2.5 m and >2.5 m (at the same time, with diameter at breast height (DBH) smaller than 6 cm. All live and dead trees with a DBH greater than 6 cm (6 cm including) were numbered and DBH was measured with a measuring tape. They were also precisely mapped using laser rangefinders and customized software (Field-Map; Monitoring and Mapping Solutions, Jílové u Prahy, Czech Republic). Canopy position of each tree was assessed (suppressed: trees with crowns below the general canopy layer and receiving mostly diffuse light and released: trees with crowns forming the general canopy layer and receiving at least 50% of full light). Also, we recorded the species of the tree and growth layer (upper, lower). Lying deadwood with thickness above 10 cm was measured using above mentioned Field-Map technology. Both ends were mapped with a laser and the diameter was measured there with a sliding scale. Average decay stage (1–5) and species was also recorded for every piece (Stokland *et al*. 2012). Height of standing deadwood with DBH over 6 cm was estimated to height categories (0 – 10m, 10 – 20m, 20 – 30m). Subsequently, the volume of deadwood (standing and lying) was calculated. We also visually evaluated distinct substrate or tree-related microhabitat (TreM) types on all live and dead standing trees based on standardized typology (Larrieu *et al*. 2018). We subsequently aggregated observations of individual TreM types (N = 29) into broader categories (N = 11; Paillet *et al*. 2017). In the next step, we selected those which are relevant for birds (cavities, cracks, missing bark and crown deadwood).

Mean canopy openness was calculated from hemispherical photographs collected at six locations within each plot. They were processed and analysed using image processing software

(WinSCANOPY; Regent Instruments, Ste-Foy, Quebec, Canada). Individual pixels were classified into sky- or leaf-dominated classes based on their spectral properties. Pixel classification results were aggregated to determine the overall mean sky fraction. Structural variables, which were significantly correlated with bird assemblage variables, are listed in Tab. 1. All tested variables are provided in Tab. A3.

Tab. 1 Forest structural characteristics, their description and summary statistics, which were significantly correlated with bird assemblage variables. All tested variables are provided in Tab. A3.

Structural variable	Description	Units	Min.	Max.	Average
Missing bark	number of trees with bare wood patches with bark loss and wood in a decay stage of less than 2,	number	1.00	65.00	17.80
Large DW	density of the large dead trees (DBH >= 500 mm, height > 1.3 m) per hectare	number of stems per hectare	0.00	130.00	28.96
DW BA	basal area of dead trees (DBH >= 60 mm)	m^2/ha	1.23	70.208	24.99
DW volume standing	volume of standing dead trees (DBH >= 60 mm, height > 1.3m)	m^3 / ha	7.00	823.00	163.88
DW volume	amount of lying and standing deadwood	m^3 / ha	37.00	943.78	93.89
Canopy openness mean	mean openness calculated from the 6 hemispherical photos evaluated in WinSCANOPY	% of canopy area	0.08	50.46	11.7

4.2.3 Age structure and disturbance history

Age structure and disturbance history reconstructions were based on a dendroecological study reconstructing disturbance histories of the surrounding region (Janda *et al.* 2017). Twenty-five living dominant trees per plot were selected using a random number generator and were cored at 1m height. One core per tree was extracted perpendicular to the slope direction and further processed by standard dendrochronological procedures. Tree-ring widths were measured with the LintabTM sliding-stage measuring device and TsapWin software (RINNTECH, Heidelberg, Germany, http://www.rinntech.com). Finally, cores were visually cross-dated and verified using

COFECHA (Holmes 1983). Mean age, median age and age of five oldest trees were calculated for each plot.

Variables, characterizing the disturbance history covering the last 250 years of individual plots (disturbance index, maximum disturbance severity, time since the maximum disturbance, mean disturbance severity, last disturbance severity, time since the last disturbance, disturbance frequency), were derived to describe the disturbance histories (their description, units and minimum, maximum, and average values are listed in Tab. 2). Disturbance variables were calculated exclusively from dendrochronological data and span the timeframe 1750 – 2000. Disturbance events were reconstructed based on the assumption that disturbance affects neighbourhood competition and, therefore, growth responses in extant individuals (Svoboda *et al*. 2014). Disturbance event severity was estimated using regression methods and allometric equations relating the aggregate present-day size of tree responders (individuals with a disturbance signal) to the original extent of the disturbance-induced canopy gap (for details see Lorimer and Frelich 1989, Trotsiuk *et al*. 2018). Severity threshold for the disturbance event was 10% canopy cover removed in a 10-year time window. We skipped the disturbance estimation after the year 2000, because it would not be representative due to the minimum sampling size in our data which excludes more recent tree recruitment. More detailed information about processing of dendrochronological data and disturbance analysis are published in Janda *et al*. (2017).

Tab. 2 Characteristics of historical disturbance calculated from dendrochronological data.

Variable name	Variable description	Units	Min.	Max.	Average
Disturbance frequency	number of disturbance events above 15% CA (canopy area removal)	amount	1.00	4.00	2.16
Time since last disturbance	time from the last historical disturbance where ≥15% canopy area was removed, to 2017, when the structure was remeasured	years	22.00	238.00	119.00
Last disturbance severity	severity of the last historical disturbance where ≥ 15% canopy area was removed	% of canopy area	15.10	91.74	42.00
Disturbance index	Shannon index calculated for each plot based on the sum of disturbance severity per each decade from 1800 to 1980	index number	0.00	01.8	0.19
Time since the most severe disturbance	time from the most severe historical disturbance to 2017, when the structure was remeasured	years	36.00	333.00	145.00
Most severe disturbance severity	severity of the last historical disturbance where ≥ 15% canopy area was removed	% of canopy area	19.5	91.74	47.00
Mean disturbance severity	mean severity of all events above 15% severity	% of canopy area	16.95	91.74	32.00

4.2.4 Bird assemblage

The data on bird assemblage composition were collected on plots from the end of April until the end of June, i.e. during the peak breeding season. Every plot was visited three times per season in 2017 and 2018. Though, we performed only two visits in 2017 on plots in localities KOP, TIC and HLI. Point counts were used as a field technique with a census point located in the centre of each plot (Verner 1985). During each visit at each point, all birds in distance of 30 m from the observer were counted for 10 min. We recorded all birds regardless of the age and sex, but the majority of records were based on acoustic signals, particularly on territorial expressions. After the arrival to a given plot, one minute was spent silently before counting started to minimize the observer's influence on bird activity (Sutherland 2006). Counts were done early in the morning (5:00 – 10:00), and only during optimal weather conditions without heavy rain and strong wind (Moning and Müller 2008).

Species with less than five incidences were excluded from analysis to improve signal-to-noise ratio. Bird count data were summarized in a species-by-plot matrix where the count of each species at each plot was considered as its abundance index. Based on this matrix, species richness (number of species per plot), Shannon diversity (Jost 2006), overall average abundance of bird assemblage (average number of all individuals per visit per plot) and assemblage composition (proportion of individual species average abundances on average abundance of the whole assemblage) were calculated for each plot. Since bird abundances varied widely among plots (6 – 29 individuals), diversity characteristics were rarefied to a common abundance level using individual-based interpolation (Colwell *et al.* 2012).

4.2.5 Statistical analysis

4.2.5.1 Influence of forest structure on bird assemblages

Generalized linear mixed models (GLMM) were used to relate overall abundance, richness, and Shannon diversity of bird assemblages to forest structural characteristics while treating the identity of individual stands as a random effect (Bolker *et al.* 2009). GLMMs with Gaussian distribution and a log link-function were used to fit diversity and abundance data, respectively. We measured 31 forest structure characteristics (Tab. A3) and many of them were strongly correlated which may lead to unstable estimates of model parameters (Dormann *et al.* 2013). Therefore, we first fit a series of 31 simple GLMMs with individual predictors to screen for pairwise relationships. Subsequently, we combined all structural characteristics in a single model using penalized GLMMs with least absolute shrinkage and selection operator penalty (LASSO). The LASSO addresses multicollinearity problems by shrinking parameters and simultaneously enforces variable selection by penalizing some model coefficients exactly to zero (Tibshirani 1996). Penalized GLMMs with reduced complexity were yielded using a gradient ascent algorithm proposed by Groll and Tutz (2014).

Distance-based partial redundancy analysis (db-pRDA) was used to evaluate the influence of forest structure on bird assemblage composition (Legendre and Anderson 1999). Bray-Curtis distances were calculated among individual plots and forest structural characteristics were used as predictors. Due to a large number of structural parameters, we first partialled-out the effect of stands and displayed residual variation in the dissimilarity of assemblages in an ordination plot. Subsequently, all forest structural variables were fit onto the ordination and their significance was

assessed individually using a series of randomization tests (9,999 permutations). Randomization scheme of the tests was restricted to permutations of plots within stands (spatial blocks) in order to account for the hierarchical structure of the data (Anderson and ter Braak 2003). Randomization tests were also used to assess significance of the whole model and ordination axes in db-pRDA. The squared correlation coefficient (r^2) was calculated for each significant variable as a goodness-of-fit statistic. Generalized additive models (GAM) were used to corroborate the results of the ordination analysis. For this purpose, an abundance index of five species with different ecological requirements were fit as isotropic smooth surfaces into ordination space using thin plate regression splines (Wood 2017).

4.2.5.2 Influence of disturbances on forest structure

Partial redundancy analysis (pRDA) on the correlation matrix of structural parameters was used to assess the influence of disturbance characteristics on forest structure. Again, the effect of stands was partialled-out to eliminate spatial autocorrelation and significance of each disturbance variable was assessed by randomization tests restricted for spatial blocks. Results of tests were considered significant at $\alpha = 0.05$. Statistical analyses were performed in R software (R Core Team 2017) using the libraries iNEXT (Hsieh *et al*. 2018), glmmLasso (Groll 2017), mgcv (Wood 2017) and vegan (Oksanen *et al*. 2018).

4.3 Forest structure and bird assemblages in spruce- and beech-dominated primary forests in Western Carpathians differ independently on disturbance regimes

4.3.1 Study area, stand selection and study plots establishment

Our study was conducted in the Western Carpathian Mountains (Slovakia), between 48.632749° and 49.523229° N and between 19.010233° and 20.118049° E, elevation of our research plots was between 769 and 1,534 m. Research plots were located inside primary forest remnants recognized by the national inventory of primary forests in Slovakia (Jasík and Polák 2011, Mikoláš *et al*. 2019). During inventory, all potential primary forest areas were visually surveyed for structural elements, typical for primary forests. Localities with signs of human

alteration were excluded. Selected stands of potential primary forests were also checked on historical maps and aerial imagery, whether the selected area was covered with forest during that period. For details, see Mikoláš *et al*. (2019).

Eighteen study stands were distributed in seven mountain ranges with the largest areas of BDPF and SDPF – the Tatra Mts. (four spruce stands), the Low Tatra Mts. (two spruce stands), the Great Fatra Mts. (two spruce and four beech stands), Low Fatra Mts. (two beech stands), the Poľana Mts. (single spruce and single beech stand), Vepor Mts. (a single beech stand) and the Orava Beskids (a single spruce stand). Most of the SDPF stands were located on intrusive and metamorphic, acidic bedrock, beech-dominated stands were very heterogeneous. Location of stands is displayed in Fig. 3.
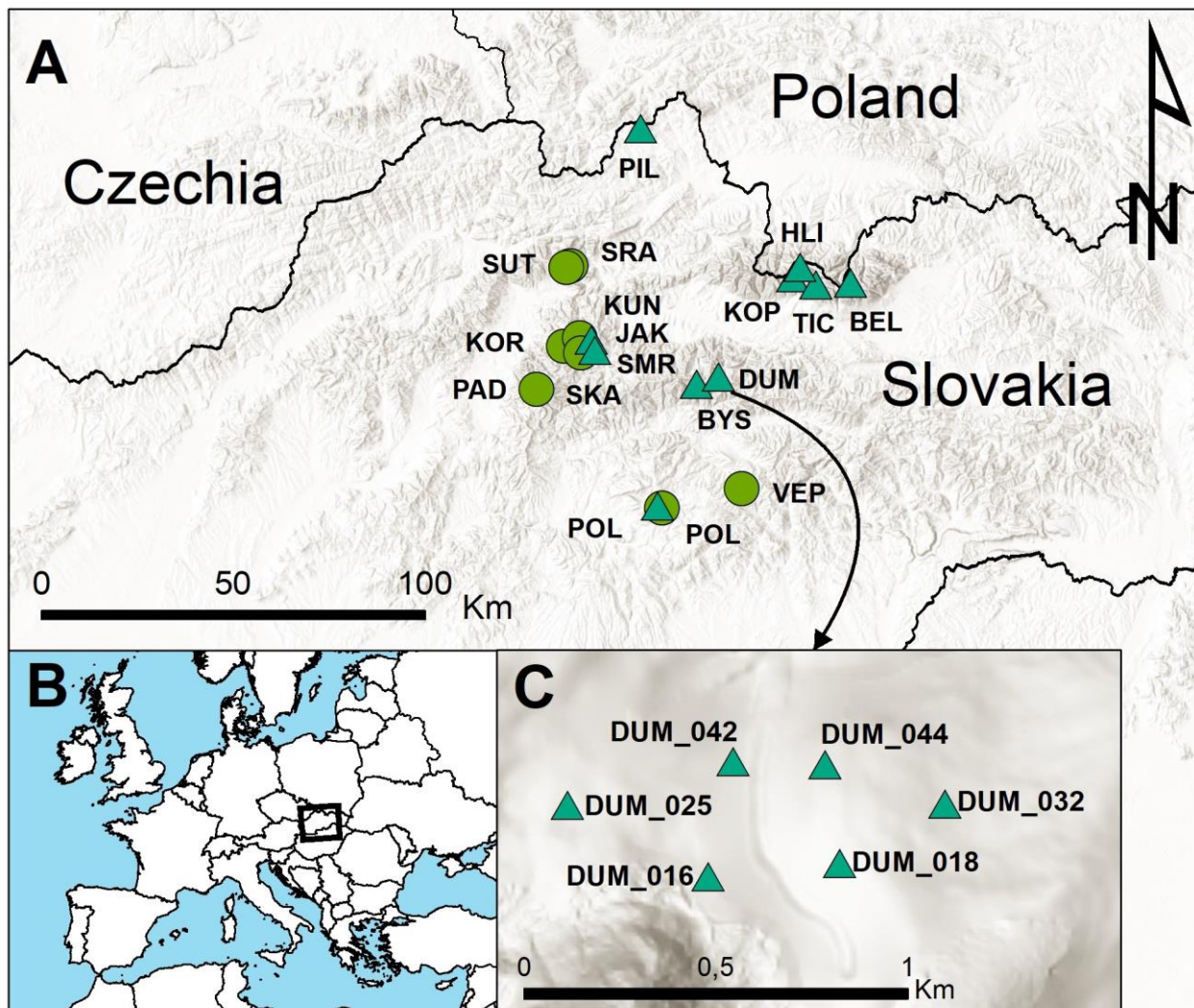
Fig. 3 a) research stands location in Western Carpathians - triangles represent spruce-dominated stands and circles beech-dominated research stands b) location of Western Carpathians in Europe, c) example of

research stand with study plots. Spruce-dominated primary forest stands: BEL (Bielovodská valley, High Tatra Mts.), TIC (Tichá valley, High Tatra Mts.), HLI (Hlina, High Tatra Mts.), KOP (Kôprová valley, High Tatra Mts.), PIL (Piľsko, Orava Beskydy), JAK (Jánošíkova kolkáreň, Great Fatra Mts.), SMR (Smrekovica, Great Fatra Mts.), DUM (Ďumbier, Low Tatra Mts.), BYS (Bystrá valley, Low Tatra Mts.), POL (Mt. Poľana). Beech-dominated primary forest stands: POL (Mt. Poľana), VEP (Vepor, Vepor Mts.), SKA (Skalná alpa, Great Fatra Mts.), KUN (Kundráčka, Large Fatra Mts.), KOR (Kornietová, Great Fatra Mts.), PAD (Padva, Great Fatra Mts.), SUT (Šútovská valley, Low Fatra Mts.), SRA (Šrámková, Low Fatra Mts.).

Size of the study sites (primary forest fragments) varied from 41 to 494 ha. In the case of the smallest fragments, we used several of them as one stand. They were surrounded mostly by forests of differing naturalness: natural forests with or without recent management or intensively managed less natural forests. Some parts are bordering with unnatural spruce plantations, salvage-logged areas and alpine habitats. However, these environmental variables were not quantified in this study.

Tree species composition in the SDPF was strongly dominated by Norway spruce (over 90%). Other species, such as rowan (*Sorbus aucuparia* L.), fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.), larch (*Larix decidua* Mill.), pine (*Pinus* spp.), and birches (*Betula* spp.), were present only as an admixture (Janda *et al.* 2017). Except of beech, BDPF stands contained highly variable proportion of other tree species mainly fir, spruce and maple, but also Norway maple (*Acer platanoides*), ash (*Fraxinus excelsior* L.), wych elm (*Ulmus glabra* Huds.), European hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.) and other species. Annual mean temperatures range from 1.6 to 3.4 ∘C in SDPF stands and from 5 to 5.5 in BDPF stands, annual precipitation varies from 1,205 to 1,365 mm in SDPF (Kozák *et al.* 2021) and around 1,067 mm in BDPF stands (Harris *et al.* 2020).

In the above mentioned 18 stands, 242 plots (97 in BDPF and 145 in SDPF) were established as a part of an international primary forest research project (www.remoteforests.org). To position plot centres, a square grid was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011) for each stand, and plot centres were placed using a stratified-random design (Svoboda *et al.* 2014, Frankovič *et al.* 2021). Within the inner part of each cell, three random points were generated. If the first point was unsuitable (e.g., rocks, water, steepness), then a second (or rarely third) randomly generated point was used. In BDPF stands, we positioned a pair of circular plots (radius of 17.84 m) along the contour, one on each side of the identified random point. Paired

plot centres were 40 m from the random point and 80 m from each other. Study plots in SDPF (radius of 12.62 or 17.84 m, depending on the stand density) were established directly on randomly generated points.

For bird assemblage and forest structure sampling, we selected 58 plots in SDPF stands (six plots per stand with the exception of one stand in the Tatra Mts. containing only four plots) and 60 plots in BDPF stands. In each stand, study plots were selected to cover the whole gradient of disturbance severities and timing over the last 250 years. For this purpose, we split plots according to disturbance event timing into three equally large classes. We then selected two plots within each class on every stand, with differing severity if available. At the same time, we avoided locating any additional plots within 150 m around a given plot to minimise multiple counts of individual birds at different plots.

4.3.2 Forest structure data

Forest structural parameters were measured in 2017 in all spruce plots and in 2020 – 2021 in beech plots. For each plot, the GPS position was recorded. All live and dead trees with a DBH>6 cm (6 cm including) were numbered and DBH was measured using a measuring tape. The trees were also precisely mapped using laser rangefinders and customised software (Field-Map; Monitoring and Mapping Solutions, Jílové u Prahy, Czech Republic). Canopy position of each tree was assessed (suppressed: trees with crowns below the general canopy layer and receiving mostly diffuse light, and released: trees with crowns forming the general canopy layer and receiving at least 50% of full light). The diameter of horizontal crown projection was measured with an ultrasound device for a sample of trees to establish statistical relationships between crown area and DBH, which was later used to estimate the proportion of disturbed canopy area.

Tree species and growth layer (upper, lower) were also recorded. Lying deadwood with thickness above 10 cm was measured using above mentioned Field-Map technology. Both ends were mapped with a laser and the diameter was measured there with a sliding scale. Average decay stage (1 – 5) and species was also recorded for every piece (Stokland *et al*. 2012). Height of standing deadwood with DBH over 6 cm was estimated to height categories (0 – 10 m, 10 – 20 m, 20 – 30 m). Subsequently, the volume of deadwood (standing and lying) was calculated. Mean canopy openness was calculated from hemispherical photographs collected at six locations within each plot. They were processed and analysed using image processing software (WinSCANOPY;

Regent Instruments, Ste-Foy, Quebec, Canada). Individual pixels were classified into sky- or leaf-dominated classes based on their spectral properties. Pixel classification results were aggregated to determine the overall mean sky fraction. Number of regenerating trees was counted on the plot-level in three height categories: 0.5 – 1.3 m; 1.3 – 2.5 m and > 2.5 m (at the same time, with diameter at breast height (DBH) smaller than 6 cm.

4.3.3 Age structure and disturbance history

For disturbance history reconstruction and age estimation, increment cores were extracted from living trees at 1 m height from the base, perpendicular to the slope direction. In spruce plots, 15 or 25 (depending on the plot radius, 12.62 or 17.84 m) randomly selected trees with DBH ≥ 10 cm and canopy status classified as currently released were sampled. If there were not enough trees on the plot, the closest trees outside the plot were selected, and rotten trees were replaced by a nearby tree with similar DBH to obtain the required sample size. An additional five randomly selected suppressed trees were cored to establish a growth-rate threshold for open canopy recruitment. In BDPF plots, a subplot with a radius of 7.99 m was established around the centre, where all trees (released and suppressed) with DBH ≥ 10 cm were sampled. In mixed beech-dominated plots, a subplot with a radius of 7.99 m was established around the centre, where all trees (released and suppressed) with DBH ≥ 10 cm were sampled. On the remaining part of the plot all released trees with DBH ≥ 10 cm and all suppressed trees with DBH ≥ 15 cm were cored, in addition to three randomly selected suppressed trees with DBH between 10 and 15 cm. Further, 12 regularly distributed points were established outside the plot within a radius of 25.23 m from the plot centre, and at each point the closest released tree with DBH ≥ 10 cm was sampled. The study plots were established as a part of the REMOTE Primary Forests network (www.remoteforests.org) and the differences in sampling design are due to the evolving needs of this long-term project.

Cores were processed using standard dendrochronological techniques and ring-width series were measured with a stereomicroscope using a LINTAB sliding table and TsapWin software (RINNTECH, Heidelberg, Germany, http://www.rinntech.com). Crossdating was performed according to the marker years approach (Yamaguchi 1991) and verified with PAST4 (www.sciem.com), CDendro (Holmes 1983, Larsson 2003), and COFECHA (Holmes 1983) softwares. For core samples that missed the pith, the number of missing rings was estimated using the method of Duncan (1989). The total number of processed cores was 5,740 (2,284 from BDPF,

3,456 from SDPF); cores that could not be properly crossdated (rotten, damaged) were excluded from further analysis, resulting in 5,092 valid core samples (1,803 from BDPF and 3,289 from SDPF).

In the next step, radial growth patterns were analysed to identify two types of tree canopy accession events: (1) release – abrupt, sustained increase in tree growth, indicating mortality of a former canopy tree, and (2) open canopy recruitment – rapid juvenile growth rates indicating recruitment in a former canopy gap (Lorimer and Frelich 1989). Releases from suppression were identified by the absolute increase method (Fraver and White 2005) as pulses where the difference between average growth rates of adjacent 10-year running intervals (absolute increase) was greater than or equal to 1.25 standard deviations of all the calculated absolute increase values. To avoid false detection when mean growth rates are largely influenced by several extreme years, increases had to be sustained for at least seven years to be considered a release event (Fraver *et al*. 2009). Variables characterising the age structure and disturbance history covering the last 250 years of individual plots were derived to describe the disturbance histories. The reconstructed disturbance chronologies were limited to 250 years (1750 – 2000) to avoid potential bias due to the small number of sampled trees originating before this period. We also skipped the disturbance estimation after the year 2000 because it would not be representative due to the minimum sampling size in our data which excludes more recent tree recruitment.

4.3.4 Bird assemblage

The data on breeding bird assemblage composition were collected on plots from the end of April until the end of June, i.e. during the peak breeding season. Every plot was visited three times per season on average, SDPF plots in 2017 and 2018 and BDPF plots in 2019 and 2020. Some plots were visited less often due to the bad weather. Point counts were used as a field technique with a census point located in the centre of each plot (Verner 1985). During each visit at each point, all birds were counted for 10 min. and recorded in two separate datasets: all birds within the estimated distance of 60 m from the observer. We recorded all birds regardless of the age and sex, but the majority of records were based on acoustic signals, particularly on male territorial expressions. After the arrival to a given plot, one minute was spent silently before counting started to minimise the observer's influence on bird activity (Sutherland 2006). Counts were done early in the morning

(5:00 – 10:00 AM), and only during optimal weather conditions without heavy rain and strong wind (Moning and Müller 2008).

4.3.5 Statistical analysis

We employed a direct ordination analysis to target our aims. Redundancy analysis – RDA (Rao 1964) on the correlation matrix of structural characteristics was used to compare structural variables important for birds in BDPF and SDPF (Fig. 2). The same approach was used to compare the disturbance history characteristics of both forest types (Fig. A1). Finally, we used distance-based redundancy analysis - db-RDA (Legendre and Anderson 1999) to test for differences in the composition of bird communities between the forest types (Fig. 3). Rarely observed bird species (frequency of occurrence < 3 plots) were excluded from the datasets to improve the signal-to-noise ratio. Species presence/absence data were converted to Sørensen dissimilarities and submitted to db-RDA. Differences between SDPF and BDPF were tested using randomization tests. Since the data were collected in a hierarchical design (plots nested within stands), we performed a spatially-restricted randomization scheme (Anderson and ter Braak 2003) where no randomization was performed at the plot level but the whole stands were freely reshuffled 10,000 times. The direct ordination analyses were performed in R (R Core Team 2021) using the library vegan (Oksanen *et al.* 2019).

5 Results

5.1 Synchronised disturbances in spruce- and beech-dominated forests across the largest primary mountain forest landscape in temperate Europe

5.1.1 Stand-level disturbance synchronisation

Exploring the whole time series using Kendall's coefficient of concordance (Fig. 4), the level of synchrony varied widely among the stands. For example, disturbance patterns of spruce plots in the Capra and Boia Mica valleys were highly synchronised (W = 0.71 and 0.58, respectively), while synchrony among spruce plots in the Sambata valley was generally lacking (W = 0.20). The beta regression showed that spruce forests have significantly higher average synchrony (z = 10.8, p < 0.001) and higher between-stand variability of synchrony (z = 14.6, p < 0.001) than the beech-dominated forests (Fig. 4). However, the differences in synchrony between the forest types were driven mainly by highly synchronised plots in the Capra and Boia Mica valleys. After removing these stands from the analysis, the average stand-level synchrony of beech-dominated and spruce forests becomes statistically indistinguishable.
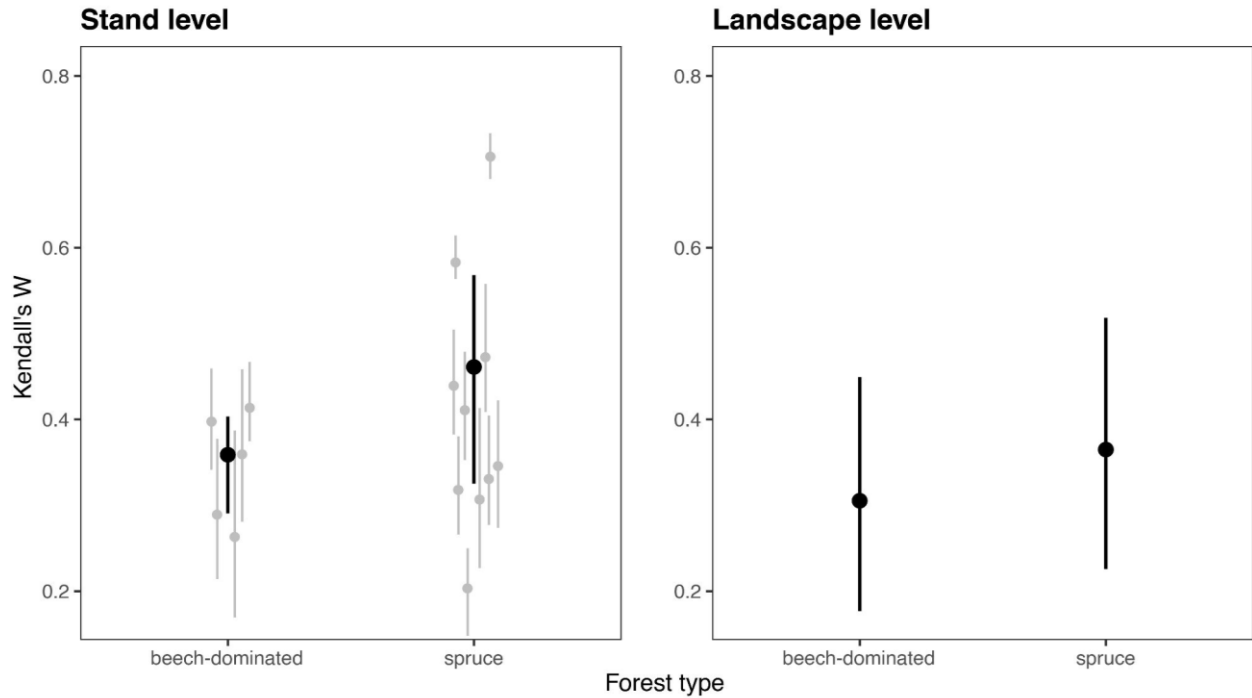
Fig. 4 Differences in synchrony of disturbance dynamics in beech-dominated and spruce forests at the stand and landscape levels. Mean values of Kendall's coefficient of concordance (black dots) are displayed along with their 95% confidence intervals (error bars). Estimates of the coefficients for individual stands and their confidence intervals are shown in grey.

In most of the beech-dominated stands (except in Arpasul valley), we found noticeable synchronised and severe disturbances around the year 1900 (Fig. A3); this was similar even in stands oriented along opposing aspects of the Făgăraș Mountains. For example, Boia Mica, a southerly-oriented valley in the western part of the mountain range, had a stand-level disturbance peak in 1893, and Belia, a northerly-oriented valley in the eastern Făgăraș Mountains, peaked in 1897. In the case of spruce stands, the synchronisation of disturbance peaks was not so pronounced as in beech-dominated stands (Fig. A4). Some of the more severe stand-level disturbances also appeared synchronised across forest types (Fig. 5).
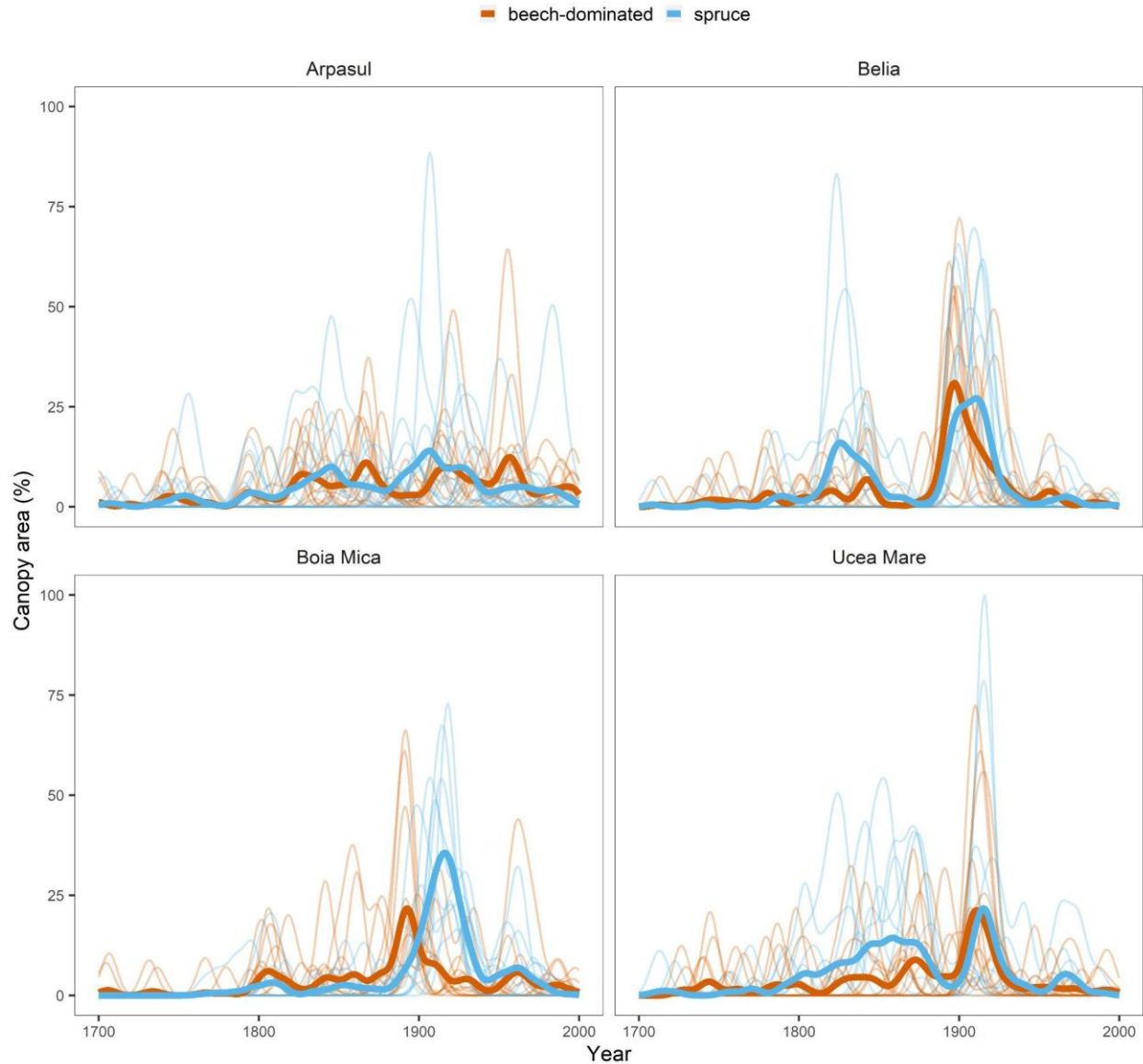
Fig. 5 Disturbance history of four valleys with the presence of both forest types (Arpasul, Belia, Boia Mica, Ucea Mare). The thick line represents the stand-level chronology plotted as a kernel density function fitted to the average disturbed canopy area of beech- (vermillion) and spruce-dominated (sky blue) plots; individual plot-level chronologies are represented as thin lines. All stand-level chronologies are detailed in Fig. A3 and Fig. A4.

5.1.2 Landscape-level disturbance synchronisation

At the landscape level, we identified temporally synchronised disturbances especially around the year 1900 (Fig. 6). Strong, synchronised disturbances were also recorded in the following two decades (1900 – 1920). According to the shapes of the plot-level chronologies,

synchronised disturbances around 1900 were most likely caused by two distinct events: one around 1890 and the second around 1910. Aside from these two high-severity synchronised events, we also found some asynchronous disturbances during this period.
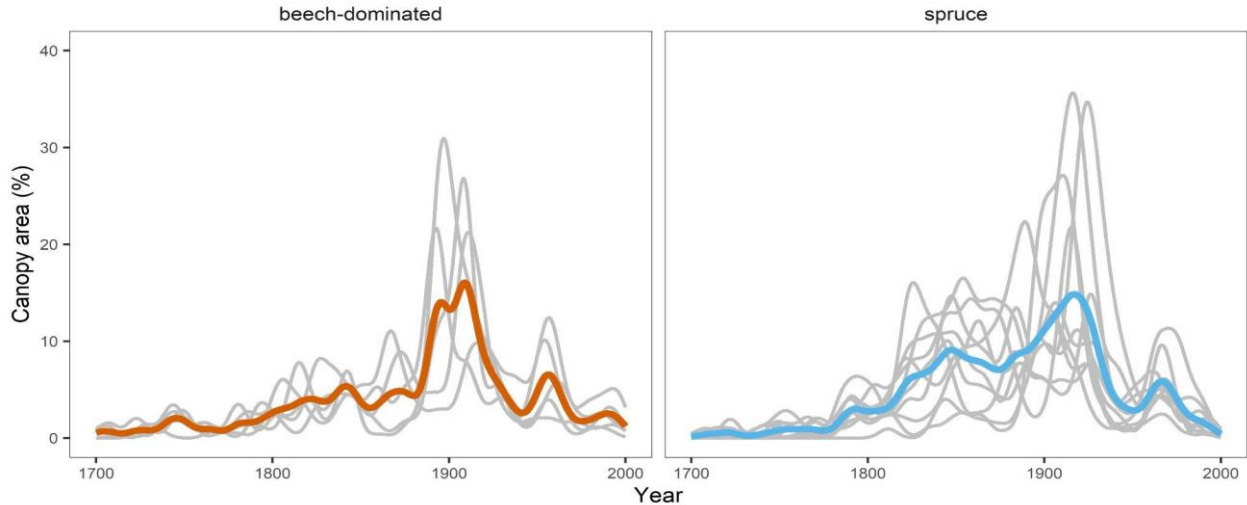
Fig. 6 Disturbance history in Făgăraş Mountains plotted as a kernel density function fitted to the average disturbed canopy area of beech- (vermillion) and spruce-dominated (sky blue) plots. Individual stand-level chronologies (grey) are detailed in Fig. A3 and Fig. A4.

Using the whole time series, Kendall's coefficient of concordance revealed a comparable degree of temporal synchrony in beech-dominated forests ($W = 0.31$) and spruce forests ($W = 0.37$) at the landscape level (Fig. 4). Disturbance patterns across the spruce- and beech-dominated forests were not synchronised more than expected by chance alone (partial db-RDA; pseudo-F = 1.16, p = 0.289).

5.2 Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition

Within the 30 m radius of all plots combined, we observed 1,045 individual birds from 23 species. The two most abundant species were the common chaffinch (accounting for 26.0% of all bird individuals recorded over two seasons) and European Robin (10.5%). Together with four other abundant species, coal tit (*Periparus ater* (Linnaeus, 1758)), Eurasian wren, dunnock and common chiffchaff, accounted for 66.0% of the assemblage (Tab. A4). In the focal forest stands we recorded

three European red listed species: Hazel Grouse (*Bonasa bonasia*), three-toed woodpecker and capercaillie.

5.2.1 Influence of forest structure on bird assemblages

We did not find any significant pairwise relationships between forest structural characteristics and Shannon diversity and species richness (Tab. A4). Also, all coefficients in penalized GLMMs were reduced to zero indicating that no linear combination of any subset of structural characteristic was useful for predicting diversity of the assemblages. We found a marginally significant negative relationship between overall abundance and mean diameter of dead trees with DBH > 60 mm, but this borderline evidence was not supported by the LASSO model. However, by examining db-pRDA (Tab. A5), we observed that composition of bird assemblages was significantly related to the number of trees with missing bark ($r^2 = 0.10$, $p = 0.034$), density of the large dead trees ($r^2 = 0.14$, $p = 0.034$), basal area of deadwood ($r^2 = 0.17$, $p = 0.007$), number of stumps ($r^2 = 0.17$, $p = 0.004$), total volume of deadwood ($r^2 = 0.20$, $p = 0.003$) and mean canopy openness ($r^2 = 0.15$, $p = 0.010$). The first ordination axis showed a gradient from more disturbed to less disturbed forest and many bird species tended to be more abundant in forest less impacted by recent disturbance (Fig. 7a). Several species showed contrasting distribution patterns along the disturbance gradient. For example, common chaffinch was more common on plots without signs of recent disturbance, as indicated by GAM response surface (Fig. 7b). In contrast, a group of five species (such as dunnock, see Fig. 7d) preferred more open habitats with a higher amount of deadwood and stumps. Coal tit (Fig. 7c) was an example of species not affected by structural variables, included in our analysis, but by some other parameter as indicated by its distinct position away from the centre of the ordination plot (see Fig. 7a). A dense group of 13 species in the middle of the ordination space did not show any consistent trend as exemplified in distribution patterns of common firecrest (Fig. 7f).
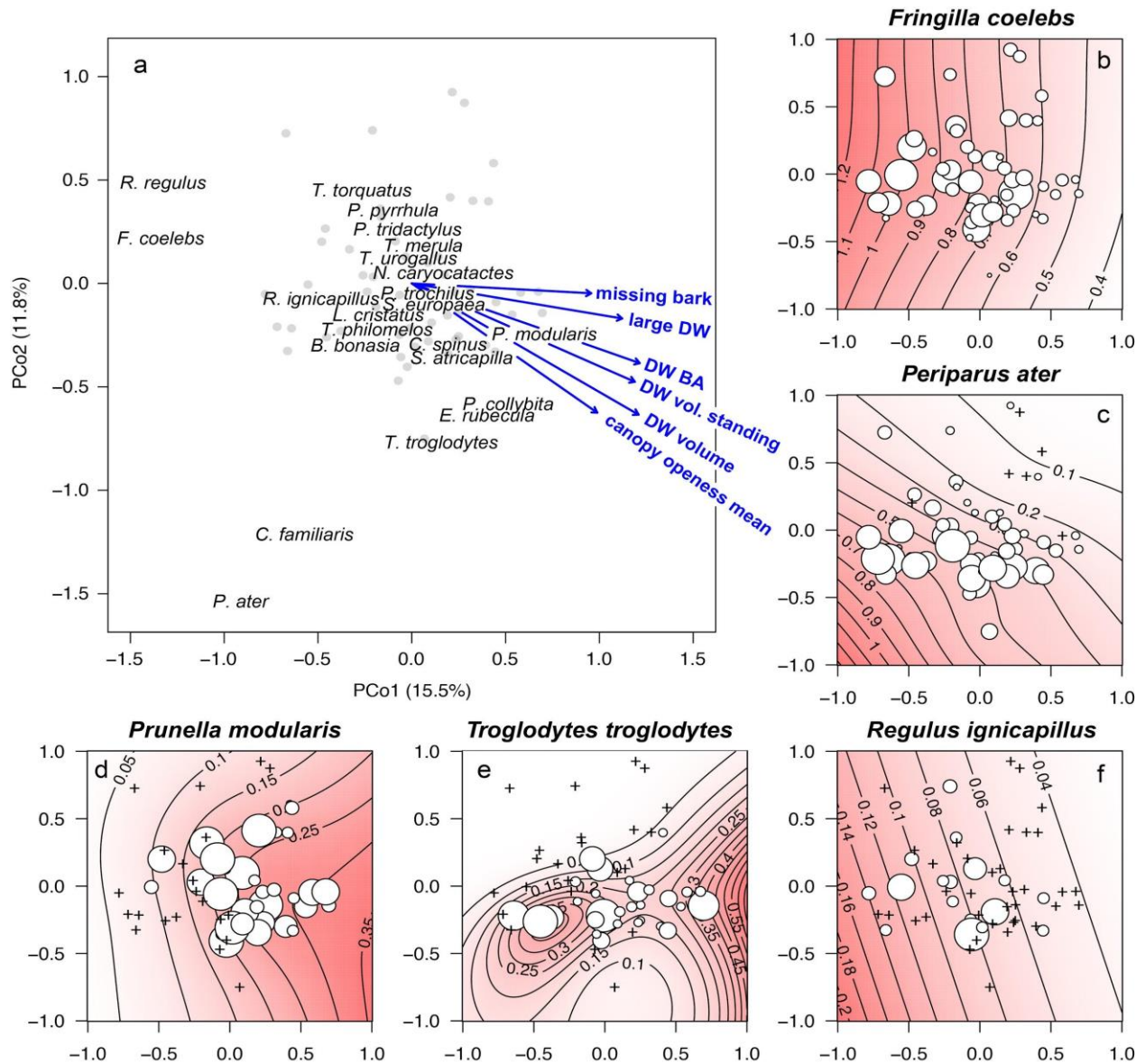
Fig. 7 Ordination plot of db-pRDA showing relationships between assemblage composition of birds and structural characteristics of primary forests that significantly correlate with configuration of ordination scores (a). Variation explained by the first two principal coordinates (PCo), after accounting for differences among stands, is given in parentheses. Subsets b–f display example species distribution patterns as predicted by GAMs. Contours represent predicted species abundances while sizes of site scores are proportional to observed number of individuals (plus signs represent absence of a given species). Ordination scores are scaled symmetrically. For details on structural variables see Tab. 1 and Tab. A3.

5.2.2 Impact of disturbances on the forest structure variables important for bird assemblage

We found that the current structure of primary spruce forests in the Western Carpathians is significantly related to the time since the last disturbance (pseudo-F = 3.23, p = 0.012), severity of last disturbance (pseudo-F = 1.84, p = 0.048) and the frequency of disturbances ≥ 15% of canopy area was disturbed (pseudo-F = 3.13, p = 0.005). Forest structural variables describing different aspects of deadwood amount were positively related to the frequency of historical disturbance events and negatively to the time since last disturbance (Fig. 8). Number of trees with missing bark was positively related to the severity of the last disturbance. Canopy openness was negatively linked with time since the last disturbance. Remaining disturbance characteristics were not significantly related to the forest structural parameters (disturbance index – pseudo-F = 0.48, p = 0.935; most severe disturbance – pseudo-F = 1.19, p = 0.233; time since the most severe disturbance – pseudo-F = 0.41, p = 0.989).
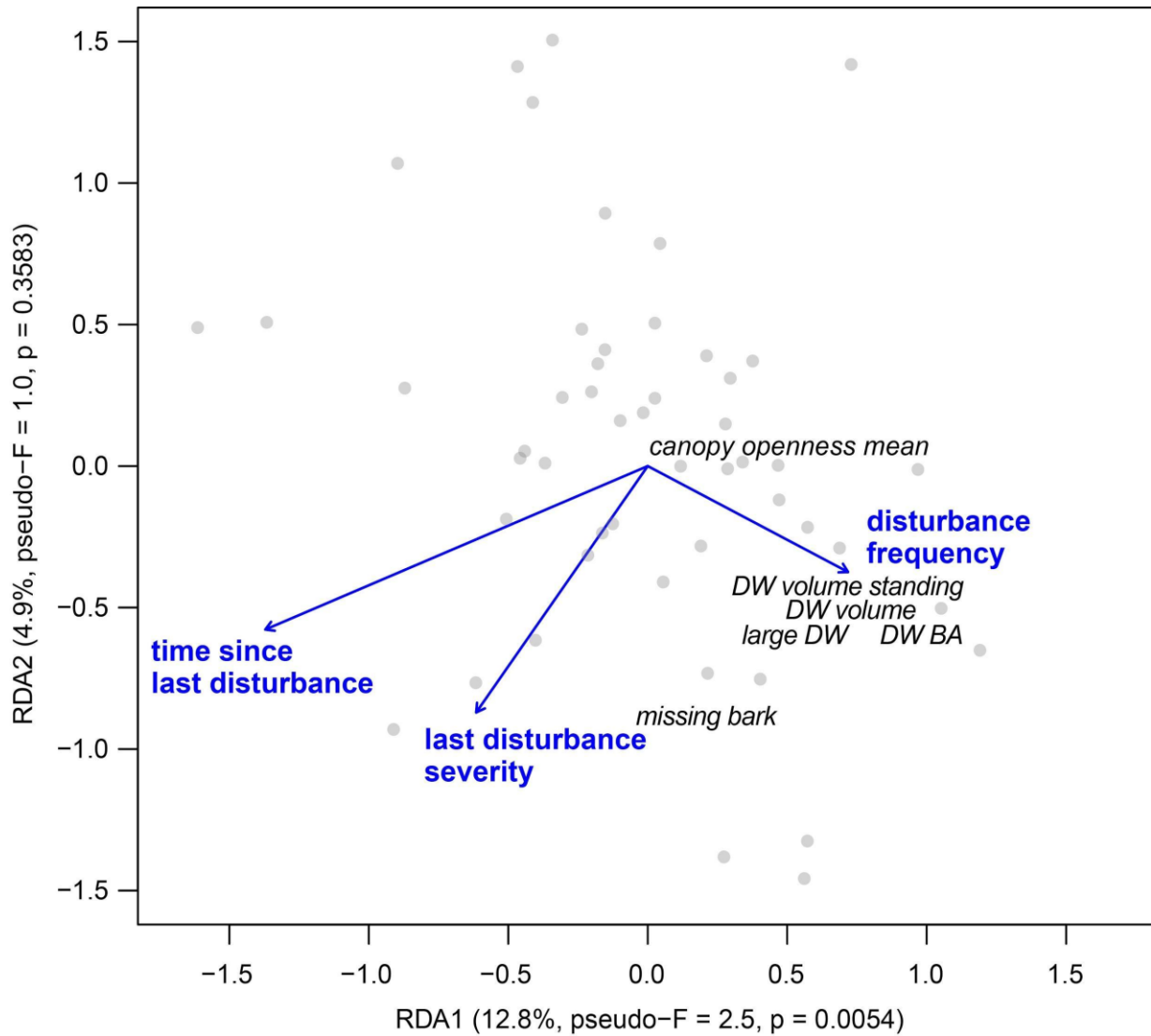
Fig. 8 Ordination plot of pRDA showing relationships between three disturbance characteristics (arrows) which significantly correlate with structure of primary forests in Western Carpathians after accounting for differences among stands. Scores of plots and structural parameters are displayed as grey dots and text, respectively. Results of randomization tests and variance explained by each axis is shown in parentheses. Ordination scores are scaled symmetrically. Note that only those structural characteristics that were significantly related to bird assemblage composition are displayed (see Fig. 7). For a full description of the variables and their abbreviations see Tab. 1 and Tab. 2.

5.3 Forest structure and bird assemblages in spruce- and beech-dominated primary forests in Western Carpathians differ independently on disturbance regimes

5.3.1 Structure in beech- and spruce dominated primary forests

The redundancy analysis revealed that the forest structure of BDPF is significantly different from the SDPF (pseudo-F = 15.1, p < 0.0001, Fig. 9). SDPF have a significantly higher density of cavities and higher canopy openness while BDPF were typical for higher tree species richness and more intense regeneration (Fig. 9). Tree density and age characteristics were more or less
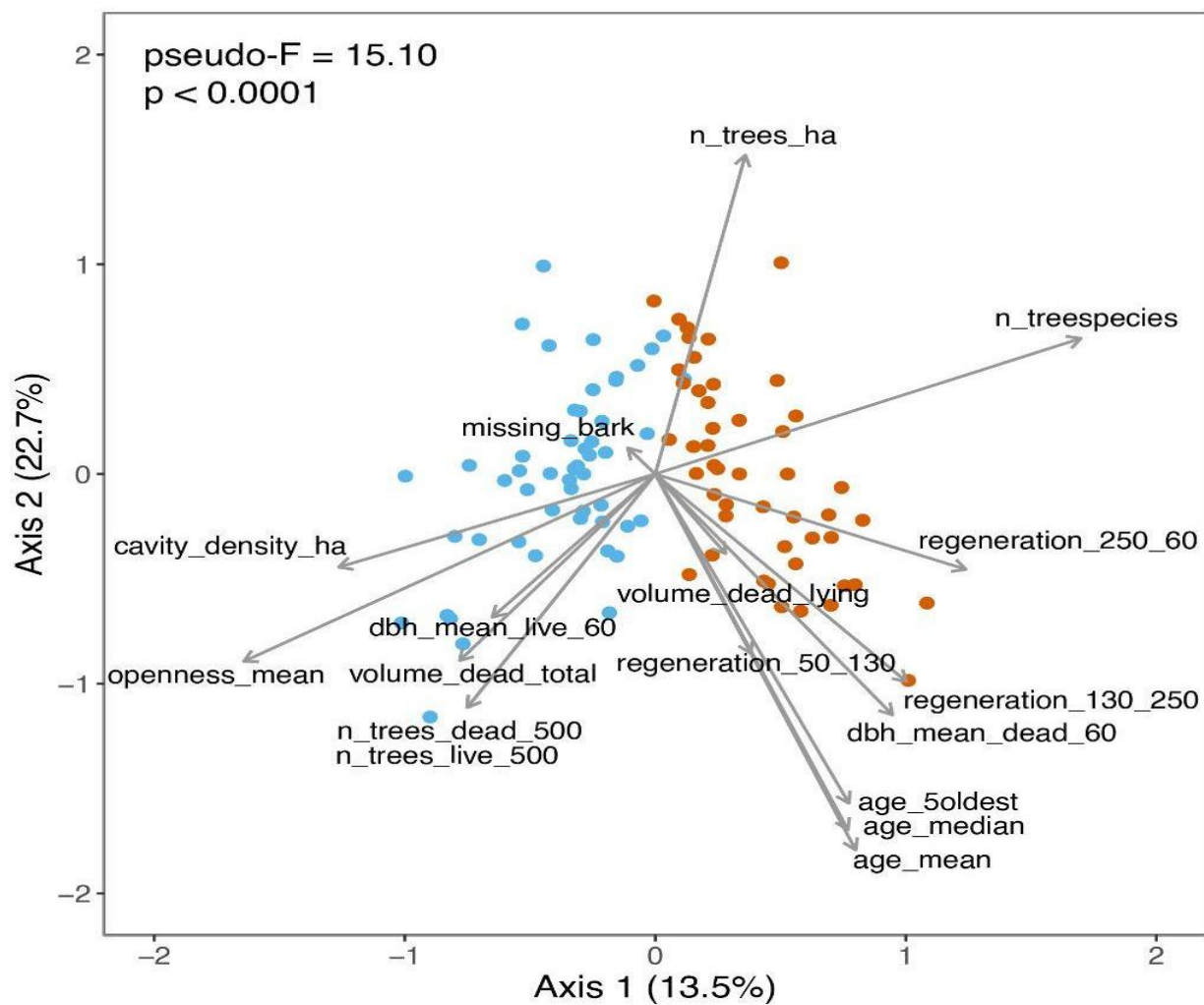
Fig. 9 Results of RDAs testing for differences between BDPF and SDPF in structural characteristics. Ordination diagrams show scores of sampling plots (blue dots- spruce plots, red dots - beech plots) and

vectors of environmental variables (arrows). The proportion of variance explained by the ordination axes is given in parentheses. The ordination plots are scaled symmetrically. Description of variables is available in Tab. A5.

comparable between the forest types. The research plots were selected to cover the whole disturbance gradient to filter out the differences in disturbance regimes and redundancy analysis showed that there are no significant differences in disturbance characteristics between our plot selection in BDPF and SDPF (pseudo-F = 1.8, p = 0.127, Fig. A5).

We found higher amounts of deadwood in SDPF (293.8 m^3/ha on average, stand level averages 144.8 – 628.3 m^3/ha), plot-level values varied between 71 – 978 m^3/ha. In BDPF it was 169.3 m^3/ha on average (stand level averages 92.2 – 254.4 m^3/ha, plot-level volumes between 12 – 628 m^3/ha). Average stand-level canopy openness was 4.4 % in BDPF (stand averages between 2.4 – 6.2%, plot level values between 1.0 – 24.9%) and 14.4% in SDPF (stand level averages 9.6 – 21.0%, plot level values between 2.9 – 50.5%). Number of trees per hectare was higher in BDPF - average on stand level reached 480, in SDPF 385 (Tab. 3).

Tab. 3 Selected structural parameters averaged on stand level.

Stand	Forest type	Elevation [m a.s.l.]	Age mean [years]	Mean canopy openess [% of canopy cover]	Total volume of deadwood [m^3/ha]	Number of dead trees with DBH over 500 mm per ha	Number of trees per ha	Number of tree species
BEL	spruce	1361	162.0	17.6	628.3	63.3	293	1.5
BYS	spruce	1416	168.3	21.0	326.5	30.0	315	1.8
DUM	spruce	1497	158.3	11.7	144.8	13.3	383	1.8
HLI	spruce	1421	129.5	13.8	285.0	40.0	460	1.3
JAK	spruce	1307	128.4	15.9	150.8	4.0	312	1.6
KOP	spruce	1409	107.2	10.9	404.0	23.3	938	2.7
KOR	beech	1117	192.9	3.6	177.3	11.6	524	3.7
KUN	beech	1091	231.0	5.7	207.0	12.4	295	3.9
PAD	beech	1161	178.2	6.2	138.3	4.5	430	3.7
PIL	spruce	1330	186.2	12.5	200.3	15.0	263	1.0
POL	beech	1144	139.8	2.4	206.6	9.4	559	4.2
POL	spruce	1377	127.5	9.6	260.3	15.0	333	2.5
SKA	beech	1165	191.9	4.7	254.4	18.4	388	2.6
SMR	spruce	1383	135.0	14.0	233.5	20.0	210	1.8
SRA	beech	1050	104.7	5.6	161.9	7.7	751	3.7
SUT	beech	1054	153.7	3.8	92.2	10.0	565	3.0
TIC	spruce	1420	112.0	17.2	304.0	38.3	338	1.5
VEP	beech	1197	149.4	3.5	116.9	7.7	323	4.1

5.3.2 Bird assemblage in beech- and spruce-dominated forests

In total, we recorded 4,745 bird individuals from 54 species. 45 species in BDPF (beech-) and 37 in SDPF (spruce-dominated primary forests). When accounted for differences in sampling intensity, we recorded a 17,3% lower number of individuals in BDPF. 29 (53,7% of all species) occurred in both forest types, but 17 out of them were more numerous in SDPF. 24 species were recorded only in single forest type - 16 in BDPF, 8 in SDPF. Species with dominance over 5% accounted for 60% of the total number of individuals in BDPF (6 species) and 74% in SDPF (8 species).

The composition of bird communities in BDPF was significantly different from the SDPF (pseudo-F = 17.6, p < 0.0001). Crested tit (*Lophophanes cristatus* (Linnaeus, 1758)), three-toed woodpecker, the dunnock, Eurasian bullfinch (*Pyrrhula pyrrhula* (Linnaeus, 1758)), ring ouzel (*Turdus torquatus* Linnaeus, 1758) and Eurasian siskin (*Carduelis spinus* (Linnaeus, 1758)) emerged as indicative for SDPF. Collared flycatcher, white-backed woodpecker, the wood warbler and the great tit and mistle trush (*Turdus viscivorus* (Linnaeus, 1758)) were typical for BDPF (Fig. 10). The common chaffinch and the European robin were the most abundant species in both forest types, other common species with high abundances were the coal tit, Eurasian blackcap (*Sylvia atricapilla* (Linnaeus, 1758)) and the Eurasian wren. For a complete list of recorded species in BDPF and SDPF with dominances see Tab. A8.
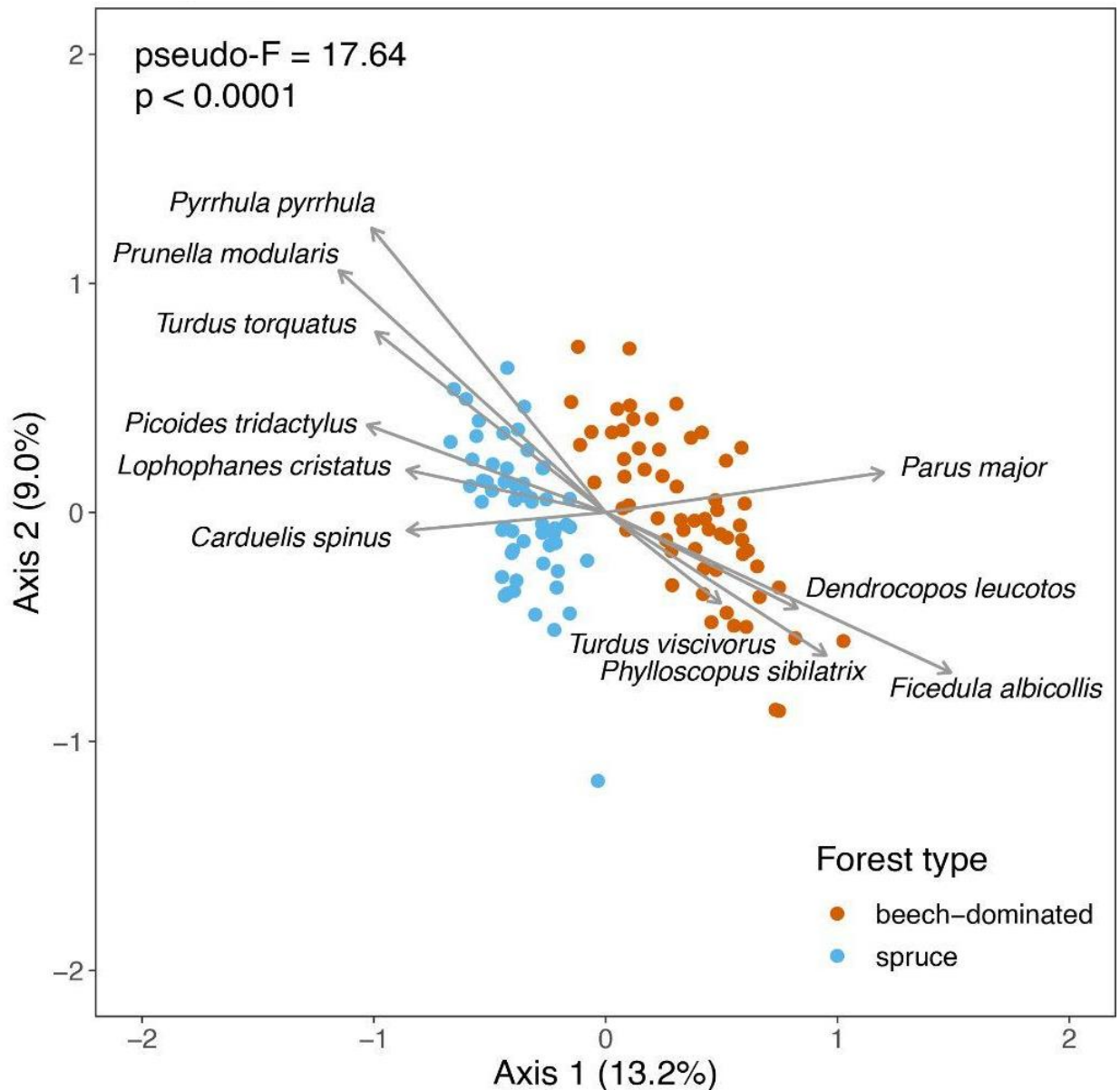
Fig. 10 Results of db-RDAs testing for differences between BDPF and SDPF in bird species composition. Ordination diagrams show scores of sampling plots (dots) and species vectors (arrows). Only species with a good fit to the ordination ($|r| > 0.4$) are displayed. The proportion of variance explained by the ordination axes is given in parentheses. The ordination plots are scaled symmetrically.

We recorded also several less numerous, but important bird species of conservation concern in Carpathians - in SPDF it was Three-toed woodpecker, the capercaillie, the Eurasian pygmy owl, the boreal owl (*Aegolius funereus* (Linnaeus 1758)), the golden eagle (*Aquila chrysaetos* (Linnaeus 1758)) and the black woodpecker (*Dryocopus martius* (Linnaeus 1758)). In BDPF we found the

Ural owl (*Strix uralensis* Pallas 1771), the peregrine falcon (*Falco peregrinus* Tunstall, 1771) and the red-breasted flycatcher (*Ficedula parva* (Bechstein, 1792)).

6 Discussion

6.1 Synchronised disturbances in spruce-and beech-dominated forests across the largest primary mountain forest landscape in temperate Europe

6.1.1 Spatiotemporal disturbance synchronisation in beech- and spruce-dominated forests

Firstly, we identified landscape-scale synchronisation of disturbance activity between both forest types, especially between the disturbance events in the three decades between 1890 and 1920. Interestingly, the disturbance peak in both forest types was also evident in the most distant valleys (air distance ca. 45 km) with contrasting expositions (northeastern and southwestern expositions; Fig. 1), which highlights the scale of synchronicity in disturbance activity across the landscape. It is important to stress that such synchronisation in the Făgăraş Mountains is quite surprising: disturbances tend to be more synchronised in flat areas, with not-so-rugged relief (Senf and Seidl 2017). The wind can blow there without obstacles, and bark beetles are also not limited by barriers of high mountain ridges and changes in tree species composition. In the Făgăraş Mountains, valleys are deep (500 – 1,000 m) and oriented at the right angle to the prevailing wind direction. It is an essential point in terms of the possibility to partially generalise our results for European mountain temperate forests, although it is not our primary goal. It seems that synchronised disturbances were occurring in primary forests regardless of the topography, probably because of other factors (drought, ice storms). On the other hand, we do not know the exact size of the disturbed area. It is most likely that the patches were synchronised but not interconnected.

Overall synchronicity of chronologies, quantified with Kendall's coefficient of concordance (Fig. 4), showed significantly higher synchronisation of disturbance chronologies in spruce-dominated primary forests at the stand level compared to the beech forests. Like the beech-dominated forests, spruce forests are also shaped by wind, and secondarily by bark beetles. After the windstorm-induced disturbance, bark beetles often multiply and attack damaged or even healthy trees in close proximity, thereby enlarging disturbance patches (Hlásny *et al*. 2021b).

However, at the landscape level, the synchronicity in beech- and spruce-dominated primary forests was comparable. Dynamics in both forest types are driven by mixed-severity disturbance regimes, where disturbances of various severities affect primary forests across large scales (Frankovič *et al*. 2021, Svoboda *et al*. 2014). Natural disturbances are highly variable within beech- and spruce-dominated primary forests throughout the Făgăraș Mountains. Although beech- and spruce-dominated primary forests are affected by disturbances in distinct ways (Fig. 4) and there are differences in the disturbance synchrony in these two forest types, we also detected considerable overlaps between disturbance events in these two forest types (Fig. 5). The common patterns are also clearly visible in the disturbance activity of beech- and spruce-dominated forests between 1890 and 1920 (Fig. 5, Fig. 6).

Along with synchronised disturbances at the turn of 19th and 20th centuries there is a noticeable lack of disturbances in the second half of the 20th century (Fig. 5, Fig. 6). We consider this pattern a direct consequence of the aforementioned synchronised disturbances. Younger trees (mainly spruce) are less prone to disturbances (Canham *et al*. 2001, Wermelinger 2004). Therefore, when most of the areas were hit by these detected severe disturbance events, age was significantly influenced (see Tab. A1, but take into account that average age was counted only from the cored trees above 10 cm DBH). The opposite situation - when long intervals without disturbances lead to synchronised disturbances later - is described in Schurman *et al*. (2018). However, this lack of disturbances can also be partly caused by the lack of the cores from small trees (DBH threshold 10 cm, see Methods). Especially in smaller gaps, it can take some time until the trees reach the DBH threshold. In larger gaps, trees grow faster, therefore this underestimation is of lesser importance.

We documented large-scale and severe disturbances in both forest types. Although this pattern is well documented in spruce-dominated forests (e.g., Svoboda *et al*. 2014, Schurman *et al*. 2018), there is much less evidence in beech-dominated forests. Large canopy openings in beech-dominated primary forests can be formed suddenly during more intense disturbances, for example, the disturbance in July 1965 in the Dinaric Alps region, which was probably the result of a massive windstorm and its localised downbursts and microbursts (Rebula 1969). It affected an area of 110,000 ha with highly variable severity, including low-severity to high-severity events, and even some stand-replacing disturbances with patch areas between 4 to 75 ha (Nagel *et al*. 2016). Similarly, in the Western Carpathians in 2014, a wind disturbance damaged more than five million cubic metres of wood, mainly beech (Kunca *et al*. 2014). These large-scale events occurred mainly

in managed forests, which are generally more prone to severe and synchronised disturbances (Thompson *et al*. 2009). Recently, there has also been evidence of synchronised high-severity disturbance activity in beech-dominated primary forests in the Western Carpathians (Frankovič *et al*. 2021). Synchronised disturbances with higher severity were infrequent, but they are critical drivers of subsequent forest development pathways and dynamics across both forest types. Our data suggest that these events are part of the range of natural variability in spruce- and beech-dominated forests.

At the stand-level, species composition also likely played a certain role in disturbance synchronisation. In spruce-dominated stands, it was relatively similar among the stands - spruce represented from 87.1 to 99.2% of the basal area, with a median 98.0% (Tab. A2). However, in the beech-dominated stands, the proportion of beech varied from 45.5 to 84.6%, with a median of 61.8%. The lowest proportion of beech was recorded in the stand Arpasul, with the remaining basal area largely represented by fir (40.7%) and spruce (10.8%). Reconstructed disturbance chronologies on the plot level (Fig. A3) showed no major synchronisations of more severe disturbance peaks, contrary to other beech-dominated stands. This is in line with previous studies, which found that mixed-species forests are in general, more resistant to natural disturbances and environmental fluctuations (Pretzsch *et al*. 2013, Jactel *et al*. 2017, Pardos *et al*. 2021). The highest proportion of beech was in Boia Mica and Sebesu, where synchronisation of disturbance peaks is evident around 1900. Even more robust synchronisation was visible in Belia, which has a lower proportion of beech, but a high proportion of spruce (18.5%). Spruce is an important gapmaker in mixed beech-dominated forests, especially when these mixed forests are neighbouring subalpine spruce forests (Orman and Dobrowolska 2017). In such cases bark beetles may spread from subalpine spruce forests to lower elevation mixed forests. They selectively kill spruce trees there, and thus they can contribute to higher synchronisation of disturbance activity between these two forest types, but also within beech-dominated forest. However, when we expressed the synchronisation with Kendall's coefficient of concordance, which takes into account not only the disturbance peaks but the whole chronology, the beech stands were more similar than the spruce in terms of the level of synchronisation (Fig. 4).

6.1.2 Disturbance agents in the Făgăraș Mountains

We attributed the synchronised disturbance activity between spruce- and beech-dominated forests to the fact that although these forest types differ in various aspects, they also share common characteristics and behave as an interconnected system. A crucial factor in synchronising beech and spruce forests is a shared susceptibility to disturbance agents, particularly windstorms (Drössler and von Lupke 2005, Mitchell 2013). Wind is the primary disturbance agent throughout the Carpathian Mountains: the most important are large-scale cyclones, which typically affect extensive forest landscapes. Conversely, convective storms are more critical at the plot and stand levels (Pettit *et al*. 2021). Although forests of the southern Carpathians are more vulnerable to local convective storms, they can also be impacted by large-scale cyclones (Pettit *et al*. 2021).

The main disturbance factors were most likely wind, with bark beetles as a secondary agent in spruce-dominated forests. Beech-dominated forests are largely shaped by wind and potentially also by ice storms. Before 1900, there are no consistent climatic datasets, including data on precipitation, temperature and wind speeds from the Făgăraș Mountains or its close surroundings (Cheval *et al*. 2020). However, data from Sibiu and Bucharest, which are 30, respectively 160 km from the mountains, show one exceptionally dry season in 1894 (Cheval *et al*. 2020), which could be a possible trigger of disturbance events in the next years, as documented from other areas (Pederson *et al*. 2014, Schurman *et al*. 2018). Severe and synchronised disturbances after 1900 were probably also amplified by drought in the region. According to long-term climatic data (Climate Change Knowledge Portal 2021), 1907 was the third driest year in Romania in the last 120 years, which is two years prior to the second peak year of disturbance in our chronology for beech-dominated forests. In the Făgăraș Mountains, the average annual precipitation was almost 200 mm (27%) lower than the long-term average; precipitation in 1903 and 1904 was also well below average, and 1905 was only average. Although 1906 was slightly above average, it probably was not enough to replenish the missing water and prepare for another dry year. This dry period likely provided unique conditions that interacted with other disturbance agents and strengthened the overall disturbance rates, primarily caused by factors other than drought (Seidl *et al*. 2017).

Regarding the possible primary disturbance agent, we searched for the information in the database "Meteorological information at the end of 19th century from Romanian newspapers" (Cheval *et al*. 2020), which covers the years 1880 – 1900, coincidentally the period with the most severe and synchronised disturbances, especially in the beech-dominated forests. We found many

records from four counties, into which Făgăraș extends. Different extreme weather situations were recorded in this time period: predominantly thunderstorms, windstorms, floods, hailstorms, several records of exceptional snow cover and extraordinarily high or low temperatures and even one tornado. However, the data are relevant mainly for the inhabited regions. Primary forests high in the mountains were not the focus of local newspapers. Therefore, it is hard to distinguish which particular events were most important for forest dynamics.

There is a possibility that high-severity synchronised disturbances in beech-dominated forests were not caused by wind but rather by ice storms. In such cases, trees are covered with a thick layer of ice, and the branches can be broken under the weight even without any significant winds (Nagel *et al*. 2016). Such an event could explain a higher number of plots with higher severity disturbances at sites near the bottoms of valleys in northern and southern valleys simultaneously. These slopes are often covered by ice-forming fog during an inverse weather system with dense fog (Rhoads *et al*. 2002). Similar patterns of high-severity disturbances on the lower parts of slopes in Carpathian beech-dominated forests were described by Frankovič *et al*. (2021). The mountain terrain with large altitudinal gradients can contribute to the rise of extreme meteorological conditions over short distances.

6.1.3 Study limitations

Despite our extensive sampling effort and a large database of dendrochronological data, we are very well aware of some of the study limitations. Although there is a clear common pattern in disturbance activity in beech- and spruce-dominated forests between 1890 and 1920 (Fig. 5, Fig. 6), spruce forests exhibited a shifted disturbance signal that gradually increases in frequency and intensity in the decades after the disturbance peaks in beech forests. This delay of disturbance signal in spruce-dominated forests can be a result of the different nature of the two types of tree canopy accession events used for the disturbance history reconstruction, release and open canopy recruitment (for details, see section 4.1.4). In beech-dominated forests, the ratio of release to open canopy recruitment events was 64%:36%, while in spruce it was 36%:64%. When open canopy recruitment events dominate canopy accession, it can cause what seems to be a delay in the disturbance event signal detectable by dendrochronological methods. The recruitment of new trees is influenced by varying species-specific and environmental conditions and it can take more than a decade until the trees reach the dimensions (height 1m, DBH 10 cm) for core extraction. Therefore,

the exact timing of the gap creation may be further confounded by the distribution of different signals across several decades (Svoboda *et al.* 2014). Moreover, beech forests tend to be more influenced by ice storms (Rhoads *et al.* 2002), while windstorms in spruce forests are usually followed by bark beetle outbreaks, as the trees newly exposed to increased solar radiation and uprooted trees are weakened and may represent ideal conditions for bark beetle population gradation (Wermelinger 2004). Thus, the shift of the disturbance signal in spruce can be also at least partly explained by secondary bark beetle disturbance, and we assume that the real overlap of disturbance peaks between beech and spruce-dominated forests could be higher. In fact, there is rather low probability that large and severe disturbances would affect only one of the two neighbouring forest types.

6.2 Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition

Our study is the first in Carpathian primary spruce forests to link bird assemblage characteristics, disturbance history, and forest structure data. Bird assemblage composition was significantly affected by forest structure, which was, in turn, driven by disturbance history. Specifically, several structural parameters (e.g. total volume of deadwood, volume of lying deadwood, density of large dead trees, number of trees with missing bark) were significantly affected by time since and severity of the last disturbance and disturbance frequency. Taken together, these results suggest that bird assemblages are likely indirectly shaped by disturbance history.

In contrast to the species composition, diversity and overall abundance of bird assemblages were not affected by the structural characteristics we assessed. This can be partly explained by species turnover along disturbance gradients and partly by generalism of some of the species. Most species are not avoiding disturbed habitats and a small group of species, typically absent in disturbed plots, was replaced by species preferring more open canopies created by disturbances (see Fig. 7). Based on these data, it seems that diversity of bird assemblages in primary forests is resistant to natural dynamics and the effect of disturbance. The effects on bird diversity are not long-lasting though. In general, our faunal data are in good congruence with previous local

ornithological research in the spruce forest ecosystem of the Western Carpathians - in Osobitá (Baláž 2008, Baláž and Kocian 2015), Polca massif (Ślizowski 1991), Skalná Alpa in Large Fatra Mts. (Saniga and Saniga 2004).

6.2.1 Impact of forest structure on bird assemblage

6.2.1.1 Bird abundance and diversity

In our analysis, we did not find any convincing evidence of recent disturbance-related structural parameters on bird diversity and overall abundance. In contrast, Thorn *et al*. (2016) reported a negative impact of recent disturbance on bird assemblage diversity in a very similar ecosystem in the Bavarian forest. This difference can be explained in several ways. Firstly, stand and landscape-scale patch mosaics and patterns, which were not included in our analysis, can also greatly contribute to species occurrence patterns (Drapeau *et al*. 2000). In theory, disturbance may either increase or decrease bird diversity depending on disturbance severity and spatial extent. Larger, more severe disturbances homogenize landscapes and therefore favour early successional species. By contrast, spatially limited, smaller disturbances creating finer patchwork of successional stages increase habitat heterogeneity and thus also bird diversity (Battisti *et al*. 2016). Considering this theoretical background, the difference between our findings and the results from the Bavarian forest is understandable. It can be explained by the fact that disturbances in the Bavarian forest affected large continuous areas with high severity, while in the Western Carpathians they created a more patchy pattern (Janda *et al*. 2017), probably mostly due to more complex terrain (Seidl *et al*. 2016). A lack of an effect on abundance can be explained by species turnover and compensatory dynamics (Korňan *et al*. 2019). For example, replacement of common chaffinch and goldcrest, species adapted to late-successional stages, by early-successional species (Eurasian Blackcap, European robin, the dunnock, Eurasian wren and common chiffchaff) stabilises the overall abundance along disturbance gradients. In other words, disturbances are maintaining a whole array of bird diversity. The important role of early successional biotopes in forests for birds and other taxonomic groups were also highlighted recently in other works (Klaus *et al*. 2010, Swanson *et al*. 2011). Taken together, natural disturbance variability is needed to preserve dynamic mosaic of ecosystem with natural biodiversity (Kotliar *et al*. 2007). Absence of a significant relationship between forest structure and bird assemblage diversity and abundance can also be partially attributed to generally high ability of species to tolerate disturbance-related

structural changes (Fig. 7). According to our results, the majority of species are generalists in terms of disturbance related structure (e.g. Spotted Nutcracker, common chaffinch, three-toed woodpecker and this prevalence of generalism is in congruence with older works from coniferous forest ecosystems (Eiberle and von Hirschheydt 1983). This generalism can be partly explained by the fact that a mixed severity disturbance regime, which includes disturbance events of different spatial scale and severity, has historically shaped this environment (Trotsiuk *et al*. 2014, Janda *et al*. 2017). As a result, most of the species can tolerate abrupt changes and are able to use different development phases of forests (McGarigal and McComb 1995, Mikoláš *et al*. 2017b). Studies of bird assemblage short-term responses to fire disturbances in North America (e.g., in New Mexico) found similar results to ours. Only some species reacted strongly to disturbance severity, but most of them were less impacted. Species richness was similar to pre- and post-fire across all burn severities (Kotliar *et al*. 2007).

6.2.1.2 Bird assemblage composition

The overall shape of the assemblage (Fig. 7) indicates that disturbance related structural parameters are the main force shaping bird assemblages. All main drivers of changes in bird assemblage composition uncovered by our analysis, i.e. basal area of deadwood, number of standing dead trees, total volume of deadwood, mean canopy openness, and the density of trees with missing bark, are connected with recent disturbance (Frelich 2002, Swanson *et al*. 2011). There is wide consensus about the short-term effects of natural disturbances on bird diversity in forest ecosystems, which is often severity-specific (Fontaine and Kennedy 2012, Gustafsson *et al*. 2019). Our findings agree with results from the formerly managed spruce forest of Bavarian national park, which was heavily impacted by disturbances in recent decades (Moning and Müller, 2008). An increase in all significant structure related factors would indicate a more disturbed plot with more light, reduced canopy cover, dense shrubs and regeneration, and higher number of uprooted trees offering nesting places for numerous understorey species.

At the species level, bird species showed strikingly different responses to the disturbance induced forest structure, as also reported in earlier studies from mountain spruce forest ecosystems in temperate Europe (Moning and Müller, 2008, Thorn *et al*. 2016). According to Moning and Müller (2008), "mature mixed montane forest species" like common chaffinch or song thrush preferred older undisturbed forest with cavity trees and avoid stands with massive regeneration,

while other species like Eurasian wren or common chiffchaff showed the opposite trend. The majority of the bird assemblage did not show a clear response to changes in forest structure which agrees with findings reported by Moning and Müller (2008). Our results show that species response to structure was of different intensity (Fig. 7): as an example of the strongest effect we can highlight the dunnock - it was furthest from the centre of ordination in the direction of the structural variables vectors. In Fig. 7d, we see that incidences were grouped significantly on plots with higher values of disturbance related variables while less disturbed plots were avoided. The reason for this disturbance affinity was because dunnock nest in dense shrubs and feed on plant seeds and insects (Myhrvold *et al*. 2015), both of which are more abundant in disturbed stands. Eurasian wren showed a weaker response to disturbance: it also preferred more disturbed forest, but it is more influenced by canopy openness and other factors that were not analysed here. Its weaker response can result from its more diversified diet and its nesting between roots of uprooted trees, fallen branches or in rock crevices, which can be present independent of disturbance histories (Myhrvold *et al*. 2015). Common chaffinch (Fig. 7b) showed a negative relationship with disturbance even though it is often considered a forest generalist species (Reif *et al*. 2013, Begehold *et al*. 2014). However, we observed it avoiding plots bearing signs of stronger recent disturbance (see the ordination in Fig. 7 where it is located opposite the early successional species). Common chaffinch's disturbance avoidance can be explained by its feeding strategy during the breeding period when it predominantly takes leaf-eating caterpillars by gleaning leaves and branches high in the canopy (Cramp 1994) which is not yet developed on disturbed sites.

6.2.2 Impact of disturbance history on forest structure

Similar to Janda *et al*. (2017), we identified time since the last disturbance and its severity together with disturbance frequency as main drivers of current forest structure. Time since the event was a more important factor likely because it gradually increases since the event, whereas the event severity is overwritten by subsequent stochastic forest processes. Disturbance frequency was positively correlated with deadwood related variables like total amount of deadwood, amount of standing deadwood and basal area of deadwood. This pattern can be explained by the deadwood decaying dynamics since the whole process of large log decomposition takes 50 – 100 years (Zielonka 2006). When the time between disturbance events is longer, most of the deadwood will be completely decomposed. In contrast, frequent disturbances lead to accumulation of deadwood

of different decay stages. Severity of the last disturbance was less clearly correlated with the number of trees with missing bark. Trees with missing bark are mostly the dead trees, killed by bark beetles. Higher amounts of dead trees can be interpreted as a more severe disturbance. As shown in Fig. 8, only part of the variability in the current forest structure was explained by historical disturbances. We attribute the unexplained variability partly to methodological constraints. As it was previously mentioned, the most recent year of our disturbance chronologies is the year 2000 (for more details see chapter 4.2.3). For the 17 (18) years prior to the present-day forest structure inventory and bird surveys, we did not have dendrochronological data. Coincidentally, in the last two decades the Western Carpathians experienced massive windstorms and bark-beetle outbreaks (Seidl *et al*. 2014), which resulted in widespread mortality in large parts of our focal stands. However, this change is not captured by our dendrochronological data. Consequently, the effects of historical disturbance were probably overwritten to some extent by recent disturbances.

6.3 Forest structure and bird assemblages in spruce- and beech-dominated primary forests in Western Carpathians differ independently on disturbance regimes

In our study we made the first attempt to compare bird assemblages, forest structure and disturbance regimes across the largest beech- and spruce-dominated primary forest (BDPF and SDPF) remnants in the Western Carpathians in Slovakia. We showed that forest structure and bird assemblages differ significantly, despite similar disturbance regimes.

6.3.1 Forest structure in beech- and spruce dominated primary forests

Natural disturbances are the main drivers of Carpathian primary forest structure (Mitchell *et al*. 2013, Kameniar *et al*. 2021, Rodrigo *et al*. 2022). Their impact on forest is shaped by climatic conditions, which changes along altitudinal gradients, and also by tree species composition. With increasing elevation, exposure to windstorms generally increases (Senf and Seidl 2017), whilst the risk of drought is less probable (Marchand *et al*. 2023). On the other hand, changes in tree species composition affects the impact of abiotic factors and also largely shapes the response to biotic

factors. In lower altitudes, forests are generally more resilient to disturbance because they are more diverse in terms of tree species and forest structures (Walker *et al.* 2004, Pardos *et al.* 2021).

Our results show that the important bird habitat structures of BDPF and SDPF significantly differ (Fig. 10), despite our study design aimed to equally represent the plot level disturbance history categories (see chapter 4.3.1 and Fig. A5). Level of canopy openness is the main structural variable differentiating between BDPF and SDPF (Fig. 9), together with the number of tree species, which shows an opposing trend. Average stand-level canopy openness varied between 9.6 – 21.0% in SDPF and 2.4 – 6.2% in BDPF stands. Other studies also report low gap proportions - a variable more frequently used to represent canopy openness - in BDPF; 1.2% in a Slovenian locality (Bončina 2000), 2.7 and 4.2% in two primary forest localities in Poland (Orman and Dobrowolska 2017), and 7 – 8% (or 15 – 16%, depending on gap characterisation) in two localities in the Slovakian part of the Eastern Carpathians (Drössler and von Lüpke 2005). We are not aware that comparable numbers have been published from SDPF. However, a study by Čada *et al.* (2020), which analysed the historical disturbance regime across central European spruce primary forests, showed that the proportion of stand disturbed varied between 25% and 75% across 69% of the researched area. Janda *et al.* (2017) found that 89.1% of the studied stands in the Western Carpathians SDPF experienced disturbance (35.6% of canopy removal) between 1840s–1860s. These results imply that canopy openness in this forest type is on average, considerably higher than in beech forests. To add, spruce forests generally have lower tree species diversity than mixed forests which plays a role in canopy openness, as lower species diversity reduces productivity (Pretzsch *et al.* 2012).

The age variables did not differ considerably between forest types; BDPF stands were only slightly older (Fig. 9). Another study, comparing BDPF and SDPF stands in the Southern Carpathians in Romania (Kameniar *et al.* in prep.) found similar results; average tree age was 158.4 and 137.5 years in BDPF and SDPF respectively. In general, beech has been proven to be the tree with the longest lifespan among four common temperate forest tree species. Fir and maple also reach higher lifespans than spruce (Pavlin *et al.* 2021).

We found higher amounts of deadwood in SDPF (293.8 m^3/ha on average, stand level averages 144.8 – 628.3 m^3/ha), than in BDPF (average 169.3 m^3/ha, stand level averages 92.2 – 254.4 m^3/ha). This difference is probably the result of higher disturbance activity in SDPF (Synek *et al.* 2020, Frankovič *et al.* 2021). Other factors which likely play a role is the significantly longer

decomposition time of spruce deadwood in comparison with beech, and colder climate in higher altitudes, which also slows wood decomposition (Weedon *et al.* 2009). In the primary forests of the Făgăraș Mts. (Southern Carpathians, Romania) the differences between deadwood amounts in BDPF and SDPF were smaller; on average it was 145.2 m^3/ha (stand-level averages 83 – 245) in BDPF, and 151 m^3/ha (stand-level averages 87 – 224 m^3/ha) in SDPF (Kameniar *et al.* in prep.). The lower total amounts of deadwood recorded in this study can be partly explained by different methodology of measuring the lying deadwood. In our study, we measured lying deadwood with higher precision, which yields higher total volumes (see chapter 4.3.2). The different ratios between BDPF and SDPF in both studies are also probably caused by higher recent mortality in SDPF in the Western Carpathians (Synek *et al.* 2020).

Our results show that BDPF reaches higher densities of regeneration than SDPF. We attribute this difference to the different regeneration strategies of the dominant tree species; specifically, spruce regenerate predominantly on downed deadwood (Korpeľ 1989). For example, a study from the Western Carpathians (Zielonka 2006) reported that large deadwood covered only 4% of the forest floor, but it was a substrate for 43% of all seedlings. It resulted in 20 times higher density of seedlings on deadwood in comparison with the mineral soil. In contrast, beech and fir regenerate predominantly on mineral soil, which allow them to use more space. It is also a possible explanation for the slightly higher number of trees per hectare in BDPF. Our results also indicate a significant difference in the density of tree cavities between forest types, with higher densities found in spruce compared to beech sites. The higher cavity density in SDPF can be attributed to the higher amount of large dead trees (Fig. 9), which are more likely to develop cavities in addition to other microsites (Kozák *et al.* in press). The population density of woodpeckers (another cause of tree cavities) is unlikely to play a significant role, as their numbers were similar in both forest types (48 in SDPF and 50 in BDPF, for details see Tab. A8).

6.3.2 Bird assemblages in beech- and spruce-dominated primary forests

In total, we recorded 54 bird species (Tab. A8). In spruce-dominated primary forests we recorded 37 species, whilst 45 were identified in BDPF stands. These results are comparable to those found in other studies which also explored beech and spruce-dominated mountain forests in the Western Carpathians. However, most of these studies were not strictly focussed on primary

forests. For instance, Baláž and Kocian (2015) found 39 species occurring in natural spruce-dominated forest, whilst Saniga (2009) reported 45 species in the SDPF of the Great Fatra Mts., including one of our research stands (Smrekovica). Differences in the number of species can be partially explained by the use of a different methodology, for example, line transects, or the timing of field visits to also record species with evening and night activity. Ślizowski (1991) recorded 38 species from the natural spruce forest in Mt. Polica in Poland, near our research stand PIL (Piľsko). Closest to the total number of species in this forest type is probably the estimate based on field study and published data, provided by Kocian *et al*. (2005). They estimated that 59 species occur in the natural spruce forest in the Slovak part of the High Tatra Mts. (Kocian *et al*. 2005). In our previous study we reported 23 species from spruce-dominated primary forests in Slovakia (Kameniar *et al*. 2021). However, in this study, which uses part of the data presented here, we took into account only the birds recorded at a distance less than 30 m from the counting points. Although this method was more suitable for analysing the influence of structure and disturbances on bird communities (due to the small plot size), it included only a fraction of recorded species, hence the lower species richness.

Similarly, our results from BDPF are in general congruence with the results of other authors, who also found more species in this forest type than in SDPF. To highlight, one long-term study conducted in the primary forest Šrámková in the Low Fatra Mts. - a site also used in this research - found 48 species (Korňan 2004). Saniga and Saniga (2004) reported 34 – 52 species from the Great Fatra Mts.; this number varied with the season with highest diversity during the summer months. Therefore, it is likely that the total number of species recorded in our study would increase with use of the line transect method, in addition to a prolonged interval of bird counting throughout the day and year.

Most of the spruce forests in the Western Carpathians are artificial production monocultures, with significantly simplified structure (Klimo *et al*. 2000). Therefore, our work adds further evidence that naturally shaped unmanaged spruce forest supports more diverse communities than spruce monocultures (Bashta 2007, Baláž and Kocian 2015, Kocian *et al*. 2015), including rare and threatened species (see chapter 5.3.2). Typically, natural spruce forests near the upper treeline are conserved, whilst the adjacent belt of natural beech-dominated forests is replaced by spruce monocultures. In such cases, the natural trend of decreasing species richness with increasing elevation (which is also visible in our results) is reversed (Baláž and Kocian 2015).

Our results showed that in SDPF, although there is higher diversity of birds in lower elevations, absolute abundance is higher. In addition, a larger part of the species shared between both forest types were more abundant in SDPF. We attribute this pattern to the fact that these species are at least to some extent specialised to spruce and therefore, they reach highest abundances in almost pure spruce forest. It partly matches with the result of Baláž and Balážová (2012), who also compared natural beech and spruce forests in one valley in the Western Carpathians: the European robin, the dunnock, the ring ouzel, common chiffchaff, willow warbler and several other less dominant species reached higher densities in spruce-dominated natural forests. In our case, also the common chaffinch, the coal tit, the goldcrest, Eurasian wren and Eurasian treecreeper were more abundant in spruce-dominated primary forest. The difference in our results is probably caused by a small sample of data in cited work and high natural spatial and temporal variability in bird communities. We suggest that our work, which is based on extensive data from 118 study plots within 18 stands distributed across seven mountain ranges, avoided these sources of bias and thus it can serve as a valuable benchmark reference in the research of bird assemblages of mountain primary forests in the Carpathians.

Differences in structures between BDPF and SDPF such as tree species composition, density of regeneration, canopy openness, and density of cavities (Fig. 9) have a direct impact on bird assemblages by providing different niche space. This is supported by our results, which showed that bird communities differ in BDPF and SDPF; species which constituted the most significant parts of the bird community occurred almost exclusively in BDPF or SDPF. This difference in bird communities between forest types can likely be attributed to the differences in tree species composition and the associated climate conditions. However, there is a difference between BDPF and SDPF bird community specialists regarding their strict avoidance of the second forest type. Specifically, in BDPF species which shaped the ordination to a highest extent were the collared flycatcher, the white-backed woodpecker, the wood warbler, mistle trush and the great tit (Fig. 10). At the same time, these species were absent in SDPF. It implies that probably any specific constellation of structural parameters (except for tree species composition) can satisfy their habitat requirements. Other studies from SDPF or natural spruce forests also report these species as very rare or missing in this forest type (Ślizowski 1991, Baláž and Kocian 2015). On the other hand, species typical for SDPF were not so strictly tied to this forest type; a few individuals also occurred in BDPF. These species were also considered as spruce or coniferous specialists in other studies:

the crested tit, the dunnock, the ring ouzel, the Eurasian bullfinch, Eurasian siskin and the three-toed woodpecker (Fuller 1995, Pechacek and d'Oleire-Oltmanns 2004, Braunisch *et al*. 2014).

This difference in the degree of avoidance between SDPF and BDPF specialists can be explained by the fact that while beech is generally rare in SDPF (Synek *et al*. 2020, Čada *et al*. 2020), spruce is a regular admixture species in BDPF (Parobeková *et al*. 2018, Orman and Dobrowolska 2017, Frankovič *et al*. 2021). In some of our beech plots spruce represented a significant part of the canopy cover (several tens of percent). Such mixed forest creates conditions suitable for spruce specialists. For example, the only two individuals of the three-toed woodpecker were recorded in two research plots in the stand Skalná Alpa, Great Fatra Mts., which are located close to a 2.5 ha patch of forest with a large proportion of recently dead large spruce canopy trees. A high density of standing dead spruce trees, which are used by three-toed woodpeckers for foraging and nesting, has been mentioned in previously published literature as a crucial structural element for this species (Pechacek and d'Oleire-Oltmanns 2004). The presence of spruce specialists in BDPF has also been documented in other studies (Saniga and Saniga 2004, Korňan and Adamík 2014, Korňan 2004).

Along with BDPF and SDPF specialists, we also recorded a number of species which occurred in both forest types, however, they occurred in different densities. In the case of several of these species, presence or absence is probably influenced by forest structure, independently of tree species composition. For example, the dunnock appeared as a species characteristic for SDPF in ordination (Fig. 10). It is considered as a species mostly tied to spruce dominated forests (Tuomenpuro 1989). However, we also observed them quite frequently in BDPF. They were typically present on recently disturbed plots with low canopy cover, high amounts of deadwood and dense regeneration, similarly with results of other studies (e.g. Moning and Müller 2008). This kind of structure is more common in SDPF, which likely causes this forest type to be preferred by the dunnock. Another species which was more prevalent in SDPF was the Eurasian wren (Tab. A8), which is also known as species of more open forest habitats (Moning and Müller 2008, Begehold *et al*. 2014), as it utilises uprooted trees for nesting (Wojton and Pitucha 2020). Naturally disturbed patches in BDPF are used by these predominantly SDPF species, because they found there suitable forest structure which is otherwise lacking in closed canopy BDPF.

The common chaffinch and European robin were the most abundant species in both forest types, but a higher number of occurrences of both species were recorded in SDPF (Tab. A8).

Probably the main reason is that these species typically prefer coniferous forests, regardless of structure (Baláž and Kocian 2015). European robins do not show very clear preferences for structure and common chaffinch is also generalistic, but more associated with habitats with large trees and high canopy cover (Begehold *et al*. 2014).

The described patterns of bird species occurrence in BDPF and SDPF are likely to change in the near future due to climate change. Even today, we are witnessing the retreat of spruce in BDPF localities - for instance, Parobeková *et al*. (2016) found that the share of spruce basal area decreased from 34 to 23% in the period 1978 – 2015 in one BDPF fragment in the Western Carpathians, and most of the spruce basal area was replaced by beech. Similar change has also been reported from other localities across Europe, where beech is expanding at the expense of both spruce and fir (Diaci *et al*. 2011, Jaloviar *et al*. 2017, Janík *et al*. 2014, Keren *et al*. 2017). Spruce mortality will probably temporarily create suitable habitats for spruce-related bird species (especially for the three-toed woodpecker and for other open-forest species), but in the long term, their share will likely decrease. Thus, SDPF species will become more restricted to SDPF, which could negatively influence their populations (Braunisch *et al*. 2014). At the same time, beech is reportedly expanding to higher elevations and thus transforming SDPF tree species composition (Saltré *et al*. 2015). As a result, we can also expect the spread of BDPF bird species to SDPF.

7 Management implications

Based on the results presented in the thesis, we propose three main management recommendations that will help to increase biodiversity potential in temperate forest landscapes: i) the conservation of remaining primary and natural forests, ii) the restoration of large areas surrounding primary forests, and to allow colonisation of native biodiversity from primary forest fragments, iii) a shift from commercial forest management to close-to-nature forestry, what includes the partial retention of disturbance legacies and structures, typical for natural forests.

As evident from the presented thesis and numerous studies of cited authors, primary forests are unique sources of information about historical development, variability, and natural biodiversity, which should be used as a reference state for all forests. Our work contributes to a wide scientific consensus that primary forests and other forests of high naturalness should be mapped and protected without exception (Sabatini *et al*. 2020). We recorded numerous bird species, which are typically missing or reach only low densities in managed forests – for example, the capercaillie, three-toed woodpecker and collared flycatcher. Structural data also show high tree ages and dimensions, large deadwood volumes, high densities of tree-related microhabitats and other characteristics, all of which are rare or completely missing in managed forests (Kameniar *et al*. 2021, Kameniar *et al*. in prep.). The biodiversity linked to these structural elements encompasses a vast number of rare and endangered species beyond birds (Kozák *et al*. 2021, Langbehn *et al*. 2021, Ferenčík *et al*. 2022).

During our study, significant progress was made in protecting the remaining primary forests in some of the studied regions. In the Western Carpathians in Slovakia, all primary forests on state-owned properties have now been protected through the recent establishment of the strict nature reserve, "Primary forests of Slovakia", in 2022. Currently, 94.5% of Slovakian primary forests are under strict protection, together with other natural forests in close proximity. However, primary forests in private ownership should also be protected using compensation schemes. On the other hand, the situation is more complicated in Romania. Field observations show that primary forest loss continues. Despite the official protection of 70,000 ha of Romanian primary forests across the country (Catalogul pădurilor virgine și cvasivirgine din România 2022), the majority of the most valuable forests remain unprotected, and large areas were logged in the last several years, including some of our permanent study plots. Because Romania is home to the largest areas of primary

temperate forests in the European Union (Luick *et al*. 2021a), it is one of the biggest priorities of the European region to ensure their protection. It could be achieved by facilitating the process of inscribing new localities into the National Catalogue by simplifying the process and through funding provision (Luick *et al*. 2021a). The protection of Romanian primary forests and specifically, the protection of the Făgăraș Mts. and other large, relatively unfragmented primary forest landscapes, is crucial. Along with their importance in the provision of ecosystem services and habitat for native biodiversity, they represent scientifically indispensable last examples of their kind. Our study (Kameniar *et al*. in prep.) is only one of the first steps which aims to describe the disturbance regime of extensive mountain temperate primary forests which spreads across several altitudinal vegetation zones. Further research is needed to better understand the dynamics of natural forests in the temperate zone of Europe to prepare for the future consequences of rapidly accelerating climate change. If this vital research should continue, the first step is to prevent further degradation of these precious localities.

We consider the protection of the last primary forests only as a first step in applying our results and the results of numerous other studies. Because they currently represent only a tiny fraction of the landscape, primary forests have a relatively small influence on providing ecosystem functions and biodiversity protection at a country level. In addition, when isolated, their biodiversity continually erodes; many species, including birds, require large unfragmented habitats to safeguard their long-term survival (Pechacek and D'Oleire-Oltmanns 2004, Mikoláš *et al*. 2016). We showed that even in the distant past, large-scale and high-severity disturbance synchronisation occurred in primary forests across large altitudinal gradients (Kameniar *et al*. in prep.). In the future, such disturbances are increasingly likely due to the intensification of climatic changes (Romeiro *et al*. 2022). They can result in primary forest homogenisation in large areas, which can cause the loss of habitat for numerous species. Therefore, primary forests should be protected with large parts of the surrounding area, ideally in the order of hundreds of square kilometres (Potapov *et al*. 2017). Primary forests could be viewed as refugia for potential large-scale restoration of surrounding landscapes. The restoration of natural ecosystems, including forests, is considered a crucial strategy to mitigate current climate and biodiversity crises, and to adapt to the inevitable consequences of these inevitable issues. Specifically, the current decade (2021 – 2030) was entitled a decade of restoration by the UN (United Nations General Assembly 2019). In 2022, the reform of Slovak national parks (where most of our Western Carpathians research stands are located) has

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already begun (Národná rada Slovenskej republiky 2021). Currently, new zonings of national parks are being proposed by national park administrations. In general, they are counting on the gradual expansion of strictly protected A zones, primarily on state-owned properties. The government should approve these zonations, and thus further expansion of strictly protected areas should be reached by cooperation with private owners. It is in line with the EU target to protect 30% of the area until 2030 (European Commission 2020) and the COP15 target to reach the same level of protection globally (United Nations environment programme 2022).

Along with these necessities to protect primary forests and other forested areas, it is evident that a large proportion of forests will have to continue with the provision of multiple services, including the supply of fuelwood and timber. Currently, production forests in temperate Europe are witnessing large-scale mortality caused by droughts, windstorms and bark beetle outbreaks (Hlásny *et al.* 2021). Natural disturbances are typically followed by widespread salvage-logging and laborious and economically unprofitable replanting. At the same time, strictly protected areas show a much lower proportion of disturbed area (Synek *et al.* 2020, Potterf *et al.* 2022) and rapid spontaneous natural regeneration (Zeppenfeld *et al.* 2015, Kameniar *et al.* 2021). This difference is, to a great extent, the result of the contrast in primary and managed forest structure. In the case of production forests, it is significantly simplified, which results in higher vulnerability to disturbance agents and a lower ability to self-regeneration.

We propose that production forests should be managed in a way which will restore and retain basic structural elements which are observed in unmanaged primary forests, for example, large pieces of standing and lying deadwood, large and old habitat trees, natural species composition, heterogeneous age and DBH structure, and gaps varying in area and degree of canopy openness (Beese and Bryant 1999, Kraus and Krumm 2013). Although there will always be a difference between managed and unmanaged forests, considerable improvements are possible in average production forests in temperate Europe. At first, it is most important to limit clearcutting and other management approaches, which result in the removal of almost all biomass and therefore, to temporally denude the forest floor. Our naturally occurring forest types have no developmental stage comparable to the clearcut area (Lindenmayer and Franklin 2002). This kind of management has many negative consequences on forest ecosystems, even when it results from post-disturbance salvage logging (Lindenmayer *et al.* 2017). Forest management emulating natural disturbances, widely used in North America, maintains ecosystem resilience to various environmental

challenges, essential elements of ecosystem function and native disturbance-adapted biodiversity (Long 2009). Another example is Silviculture with Birds in Mind (SBM), a system increasingly employed in parts of North America. SBM emulates natural disturbance effects which directs forest development processes to provide the full complement of stand structures and seral habitats associated with the regional diversity of forest-dwelling bird guilds. While improving conditions for birds and other wildlife, the suite of SBM methods helps maintain high carbon stocking and may, through increased heterogeneity, enhance forest resilience to climate change (Thom and Keeton 2020). Similar approaches could be adapted to the dynamics of Carpathian spruce systems (Nagel *et al*. 2013, Brang *et al*. 2014, Schutz *et al*. 2016).

We urgently call for these forest management changes because accelerating climate change amplifies the negative consequences of intensive commercial forest management. In the future, we can face problems even with natural forest regeneration (Rammer *et al*. 2021, Neary *et al*. 2022). However, increasing forest biodiversity by the proposed actions will likely greatly improve their long-term resilience, which is inevitable for human society.

8 Conclusions

The findings of the presented dissertation thesis contribute to the scientific knowledge on the disturbance history and its effect on forest structure and bird communities in primary mountain forests. Particularly, the thesis provides emphasis on: i) historical disturbance regime in beech- and spruce-dominated primary forest landscape, ii) the influence of historical disturbances and forest structure on current bird communities, iii) comparison of structural characteristics and bird communities in beech- and spruce-dominated forests.

We described for the first time the disturbance regime in a single large, beech- and spruce-dominated primary forest landscape, with a special focus on spatiotemporal synchronisation. These forest types differ in various aspects, but they also share common characteristics and together behave as an interconnected system. We identified periods of synchronised disturbances across both forest types and the whole landscape. Our results emphasise the highly variable nature of mountain forest dynamics across different forest vegetation types, including infrequent severe and synchronised disturbance events. Forest dynamics is often the result of the interaction of multiple disturbance factors, and they occasionally disrupt prior existing small-scale disturbance patterns. As the climate is becoming more extreme and disturbances are expected to intensify, we need to be aware of the whole historic array of disturbances and the possibility of their future amplification (Seidl *et al*. 2017). A basic management strategy to confront future extremes and prevent homogenization of forest landscapes should include enlarging protected areas to a size that encompasses complex forest landscapes that allows for natural processes to act across multiple forest vegetation types and thereby sustain native biodiversity and ecosystem functioning. To restore natural landscapes, it is critical to consider the synchronous and asynchronous disturbance patterns beyond single forest vegetation types into the management systems intended to mimic the natural variability and interactions of disturbances.

We made the first attempt to link bird assemblage overall abundance, diversity and species composition with historical disturbance detected by dendrochronological tools. This approach is widely applicable to different taxa across a range of similar forest ecosystems (Mikoláš *et al*. 2017, Kozák *et al*. 2021). Our large-scale research covered some of the best preserved spruce primary forest in Central Europe and thus, may serve as a benchmark reference for future studies in the area. From the management perspective, our results show that natural disturbance dynamics are

maintaining native biodiversity and its complexity and therefore disturbance is a crucial aspect of Central European temperate mountain spruce forest (Janda *et al.* 2017). Therefore, forest disturbance dynamics should be accepted as natural and necessary processes of protected areas management, even though this view is still not applied in many regions of Europe (Mikoláš *et al.* 2019, Luick *et al.* 2021a). Natural dynamics may lead to a gradual restoration of natural forest features in previously managed forest (Kulakowski *et al.* 2016, Paillet *et al.* 2015) and increased biological and environmental value, as it was shown in protected forest areas in Central Europe (Müller *et al.* 2008, Lábusová *et al.* 2019, Braunisch *et al.* 2019).

From the climate change perspective, our results do not add to the recent concerns about the ability of forests to withstand increased frequency and severity of disturbances in the ongoing age of rapid climate change. Instead, our results indicate that large synchronised disturbances were part of the disturbance regime for at least the last three centuries and forest cover and bird community still have ability to recover after them. However, if the disturbances will hit larger continuous areas of forests with higher severity in the future, there is a high probability that currently strictly protected areas will not be large enough to include all forest developmental stages in sufficient areas and hence they will not safeguard the needs of a full range of native biodiversity. Therefore, we see large-scale conservation and restoration of dynamic natural ecosystems as an increasingly important part of strategy to face global biodiversity and climate crisis.

We presented the analysis of an exceptional dataset which describes forest structure and bird communities in two forest types of major importance in Central Europe in their primary state. Our results from best preserved temperate primary forests can serve as an important benchmark reference for forest management and conservation strategies focused on biodiversity conservation. We showed that bird communities and forest structure differ in beech- and spruce-dominated forests, independently of disturbance regime. Both forest types with their high tree age, high standing and downed deadwood volumes and multiple tree related microhabitats provide important habitat opportunities for numerous rare bird species, which highlights the important role of primary forests for biodiversity conservation. Thus, protecting existing primary forests, allowing managed forests to attain older ages, and increasing the heterogeneity and availability of primary forest structures in the landscapes are necessary to maintain diverse beech and spruce forest communities in times of accelerating environmental change.

9 Literature

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Appendix

Tab. A1 Selected parameters showing high ecological value of Făgăraș Mountains forests. Downed deadwood volume was measured along five transects, each 20 m long, with azimuth of 0°, 72°, 144°, 216°, and 288°. All pieces of deadwood with diameter ≥ 10 cm were identified. Standing deadwood volume was calculated as the total volume of all dead standing trees with DBH ≥ 10 cm. Regeneration of trees (young trees between 0.5 and 2.5 m height) was counted on the whole plot. Biomass was calculated as a sum of the root, stem, branch, and foliage biomass of the living trees (DBH ≥ 10 cm), calculated according to (Forrester *et al*. 2017). Wherever possible, we used equation number four with parameters selected from the appendix to best fit to our data (Forrester *et al*. 2017; otherwise, we used equation number 3).

Stand/forest type	Average tree age [years]	Age max. [years]	Number of trees with age over 270 years per hectare	DBH max. [cm]	Average number of trees per hectare with DBH over 70 cm	Average volume of downed deadwood [m³/ha]	Average volume of standing deadwood [m³/ha]	Average biomass volume [t/ha]	Average number of regeneration per hectare
Arpasul/beech	155	412	19	109	24	166	79	416	282
Belia/beech	152	429	14	108	26	61	52	477	294
Boia Mica/beech	160	505	24	132	34	62	21	538	343
Sebesu/beech	161	453	17	108	26	71	31	479	558
Ucea Mare/beech	164	438	16	103	29	119	64	469	907
Arpaselu/spruce	130	415	5	91	13	190	34	410	NA
Arpasul/spruce	141	401	15	88	11	148	66	400	242
Belia/spruce	147	303	2	81	5	67	45	392	146
Boia Mica/spruce	112	276	2	111	8	85	36	379	414
Capra/spruce	100	201	0	117	17	56	31	488	181
Doamnei/spruce	156	357	5	86	9	126	49	356	166
Sambata/spruce	146	321	2	78	2	90	67	368	209
Ucea Mare/spruce	149	327	8	83	7	106	48	381	220
Ucisoara/spruce	144	321	5	91	7	74	34	397	77
Vistea Mare/spruce	150	319	8	88	8	113	45	425	143

Tab. A2 Tree species composition in research stands, based on plot-level data.

stand/foresttype	[% of basal area] Abies	Acer	Fagus	Picea	Others
Arpasul/beech	40.7	2.3	45.5	10.8	0.6
Belia/beech	24.9	1.8	54.8	18.5	0.0
Boia Mica/beech	10.1	0.8	84.3	1.5	3.3
Sebesu/beech	13.0	1.4	84.6	0.6	0.3
Ucea Mare/beech	26.7	5.7	61.8	5.7	0.0
Arpaselu/spruce	2.4	0.1	0.0	97.1	0.4
Arpasul/spruce	5.0	1.1	0.1	93.8	0.1
Belia/spruce	0.6	0.2	0.0	99.2	0.0
Boia Mica/spruce	9.4	0.7	0.1	87.6	2.2
Capra/spruce	0.0	0.6	1.0	98.1	0.4
Doamnei/spruce	0.8	0.5	0.0	98.4	0.2
Sambata/spruce	0.6	0.2	0.0	99.1	0.1
Ucea Mare/spruce	1.9	0.5	0.0	97.3	0.3
Ucisoara/spruce	0.5	0.9	0.0	98.5	0.1
Vistea Mare/spruce	0.6	1.3	0.0	97.9	0.2

Fig. A1 The optimal cutpoint (DBH = 26.9 cm) separating subcanopy (class = 0, n = 2,191) and canopy (class = 1, n = 5,314) trees based on minimising the absolute difference of sensitivity and specificity (sensitivity = 0.90, specificity = 0.90, AUC = 0.97). The analysis was performed in R (R Core Team 2021) using the library cutpointr (Thiele and Hirschfeld 2021).
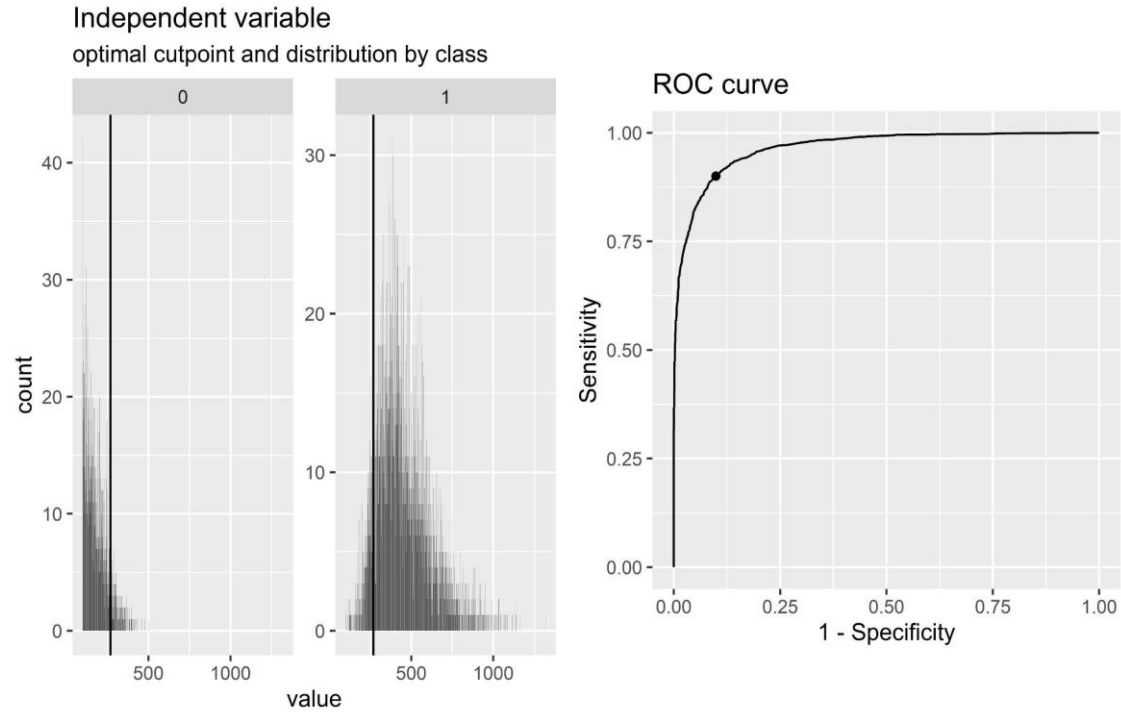
Fig. A2 The optimal cutpoints (OC) for each major species group representing the early growth-rate thresholds (mm), separating trees originating under closed (class = 0) and open (class = 1) canopy conditions based on minimising the absolute difference of sensitivity and specificity: Abies (OC = 1.536, sensitivity = 0.64, specificity = 0.66, AUC = 0.68), Acer (OC = 2.206, sensitivity = 0.72, specificity = 0.60, AUC = 0.79), Fagus (OC = 1.427, sensitivity = 0.66, specificity = 0.66, AUC = 0.70), Picea (OC = 2.125, sensitivity = 0.59, specificity = 0.59, AUC = 0.62), and Others (OC = 2.266, sensitivity = 0.68, specificity = 0.67, AUC = 0.79). The analysis was performed in R (R Core Team 2021) using the library cutpointr (Thiele and Hirschfeld 2021).
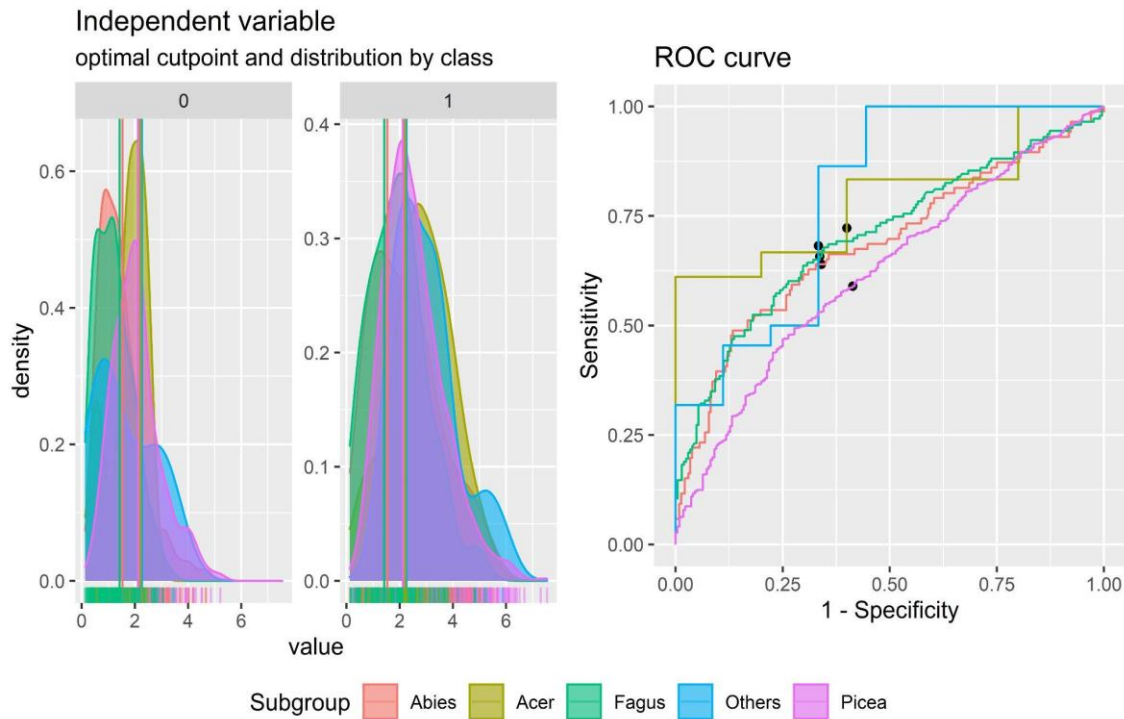
Fig. A3 Disturbance history of beech-dominated stands (Arpasul, Belia, Boia Mica, Sebesu, Ucea Mare) plotted as a kernel density function fitted to the average disturbed canopy area of beech-dominated plots. Individual plot-level chronologies are shown in grey, average stand-level chronologies are in vermillion.
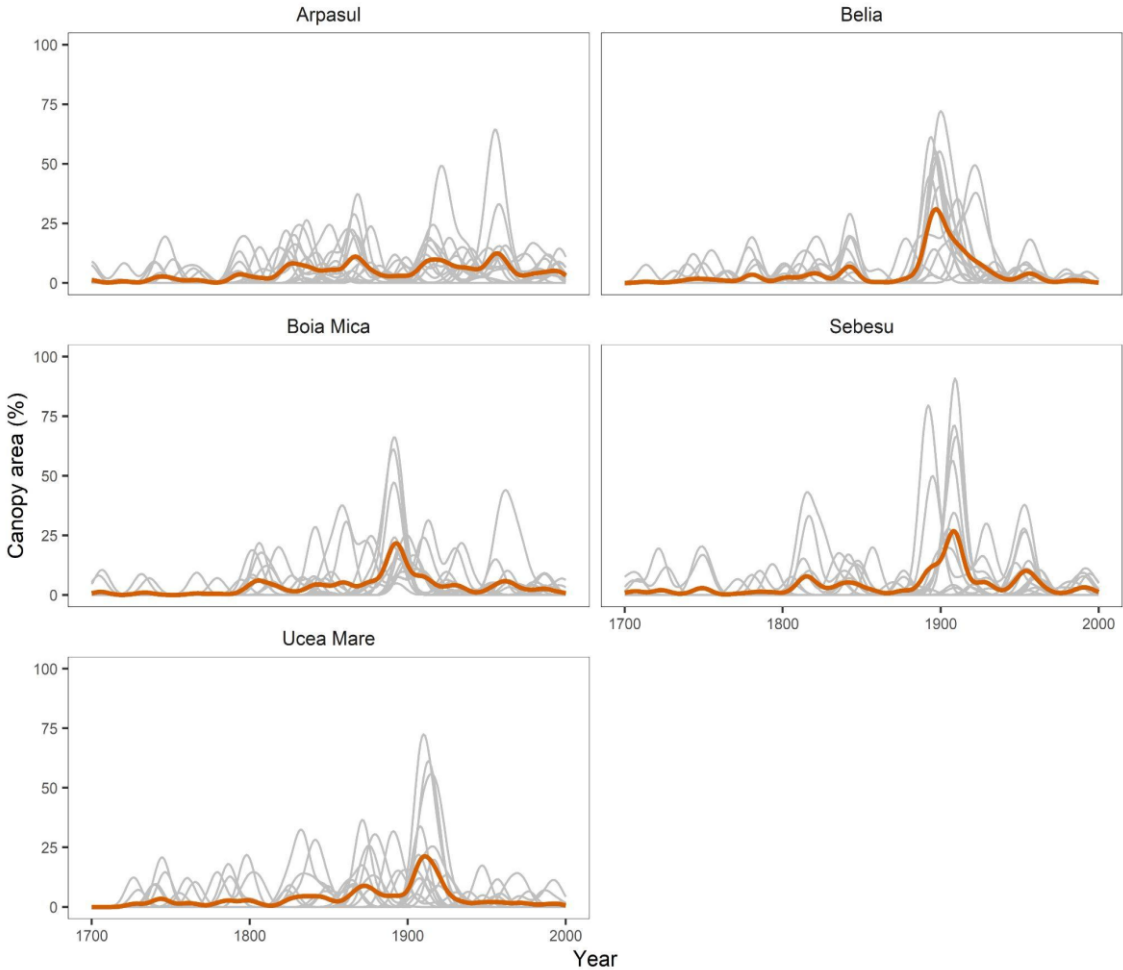
Fig. A4 Disturbance history of spruce-dominated stands (Arpaselu, Arpasul, Belia, Boia Mica, Capra, Doamnei, Sambata, Ucea Mare, Ucisoara, Vistea Mare) plotted as a kernel density function fitted to the average disturbed canopy area of spruce-dominated plots. Individual plot-level chronologies are shown in grey, average stand-level chronologies are in sky blue.
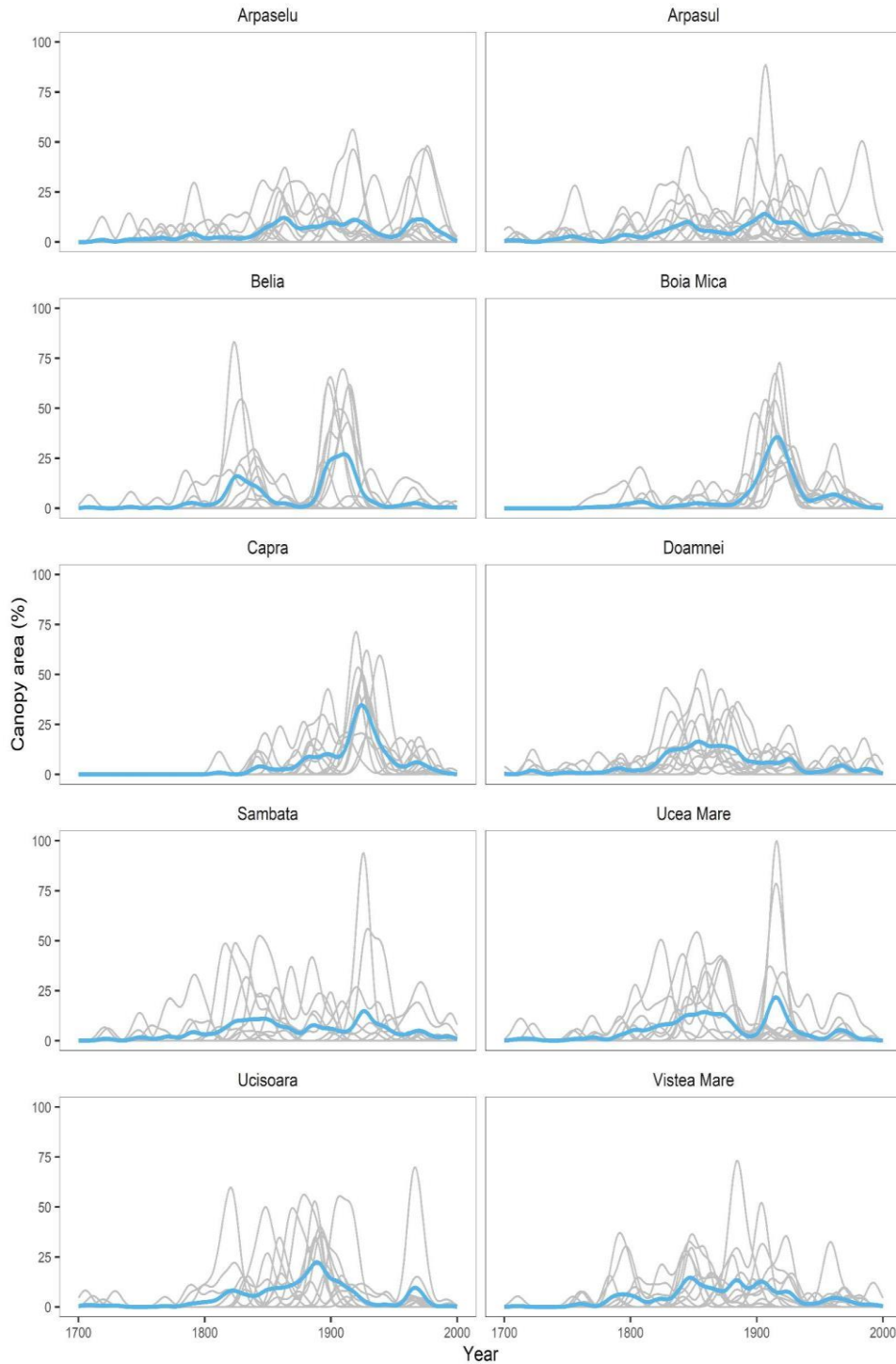
Literature

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Thiele, C., Hirschfeld, G. 2021. cutpointr: Improved estimation and validation of optimal cutpoints in R. J. Stat. Softw. 98, 1–27. https://doi.org/10.18637/jss.v098.i11.

Tab. A3 All analysed structural variables with their description.

Structural variable	Description	Units	Min.	Max.	Average
Missing_bark	number of trees with bare wood patches with bark loss and wood in a decay stage of less than 2,	number	1,00	65,00	17,80
Large_DW	density of the large dead trees (DBH >= 500 mm, height > 1.3 m) per hectare	number of stems per hectare	0,00	130,00	28,96
DW_BA	basal area of dead trees (DBH >= 60 mm)	m^2/ha	1,23	70,21	24,99
DW_volume standing	volume of standing dead trees (DBH >= 60 mm, height > 1.3m)	m^3/ha	7,00	823,00	163,88
DW_volume	amount of lying and standing deadwood	m^3/ha	37,00	943,78	93,89
Canopy openness mean	mean openness calculated from the 6 hemispherical photos evaluated in WinSCANOPY	% of canopy area	0,08	50,46	11,70
Vol_logs_all	volume of lying deadwood	m^3/ha	26,84	402,86	14,50
DBH_quadrmean_dead_60	quadratic mean of the dead trees (DBH >= 60 mm, height > 1.3 m)	mm	139,77	630,81	357,93
N_trees_live_500	density of the large living trees (DBH >= 500 mm) per hectare	number of stems per hectare	0,00	150,00	69,03
N_trees_live_700	density of the large living trees (DBH >= 700 mm) per hectare	number of stems per hectare	0,00	70,00	13,87
N_trees_dead_700	density of the large dead trees (DBH >= 700 mm, height > 1.3 m) per hectare	number of stems per hectare	0,00	120,00	8,06
N_trees_dead_60	density of the dead trees (DBH >= 60 mm, height > 1.3 m) per hectare	number of stems per hectare	0,00	700,00	170,97
N_trees_live_60	density of the living trees (DBH >= 60 mm) per hectare	number of stems per hectare	40,00	2100,00	417,74
DBH_mean_live_60	mean diameter of the living trees (DBH >= 60 mm) [mm]	mm	116,50	516,17	355,24
DBH_mean_dead_60	mean diameter of the dead trees (DBH >= 60 mm, height > 1.3 m) per hectare	mm	127,38	581,00	324,22
DBH_max_live_60	maximum diameter of the living trees (DBH >= 60 mm)	mm	148,00	861,00	662,84
DBH_max_dead_60	maximum diameter of the dead trees (DBH >= 60 mm, height > 1.3 m)	mm	209,00	940,00	609,20
Age_5oldest	age of 5 oldest living trees (DBH >= 60 mm)	years	72,20	300,60	184,79
Age_median	median age of living trees (DBH >= 60 mm)	years	36,00	225,00	125,47
Age_mean	mean age of living trees (DBH >= 60 mm)	years	32,00	210,54	130,63
Openness_gini	Gini coefficient of the openness calculated from the 6 hemispherical photos evaluated in WinSCANOPY.	% of canopy cover	0,03	48,32	2,60
Sum_cavities10	density of tree cavities per hectare	number per hectare	0,00	16,00	3,83
Sum_cracks60	density of cracks per hectare	number per hectare	0,00	24,00	6,87
Sum_crowndeadwood70	density of trees with dead branches per hectare	number per hectare	0,00	15,00	2,73
Sum_others80	density of other types of microsites per hectare	number per hectare	0,00	22,00	3,10
Trem_density_ha	density of all types of tree microsites per hectare	number per hectare	60,00	1420,00	538,33
Regeneration_0_50	density of the regeneration (0 - 50 cm height) per hectare based on the five on five 4 m2 subplots	number of stems per hectare	0,00	38000,00	4887,10
Regeneration_250_100	density of the regeneration (height > 250 cm, DBH < 100 mm) per hectare based on the data of the whole 1000 m2 plot	number of stems per hectare	0,00	680,00	71,94
Regeneration_130_250	density of the regeneration (130 - 250 cm height) per hectare based on the data of the whole 1000 m2 plot	number of stems per hectare	0,00	1200,00	191,29
Regeneration_50_130	density of the regeneration (50 - 130 cm height) per hectare based on the data of the whole 1000 m2 plot	number of stems per hectare	0,00	3760,00	472,26

Tab. A4 Bird species density (no. of breeding pairs/10 ha) on stand level. Density was calculated from the average number of territorial males observed within 60 m radius from the observer.

Species	Density on stands									
	BYS	DUM	BEL	KOP	TIC	HLI	PIL	SMR	JAK	POL
Tetrao urogallus		0.2					0.5	0.2	0.2	
Tetrastes bonasia	0.2	0.7	0.5		0.3	0.7	0.2	0.2	0.2	0.5
Columba palumbus		0.5		0.3		0.7	0.7			1.1
Cuculus canorus	1.0				0.8	0.4	1.1	0.7		0.5
Scolopax rusticola							0.5	0.5	0.5	
Buteo buteo										1.1
Glaucidium passerinum				0.5		0.4		0.5		
Aegolius funereus								0.2		0.2
Picoides tridactylus	1.7	0.5	0.3	0.3	0.5	0.4	2.2	2.2	1.2	1.7
Dendrocopos major							0.2			
Dryocopus martius	0.2						0.2	0.2		
Garrulus glandarius		0.2						0.2	0.5	
Nucifraga caryocatactes	2.5		2.9	1.3	0.3	0.7		0.2		
Corvus corax								0.2		
Periparus ater	6.4	8.4	7.2	7.1	5.6	2.9	6.1	3.7	5.2	8.4
Lophophanes cristatus	1.1		0.5	0.8	0.8	0.4	0.7	1.5	0.2	2.2
Phylloscopus trochilus	0.2	0.5	0.5	0.8	0.5	0.4	0.5	0.2	3.9	0.2
Phylloscopus collybita	4.9	1.2	6.7	5.4	6.2	5.2	2.7	4.2	2.9	3.9
Sylvia atricapilla	3.2	2.2	1.9	0.5	1.6	2.6	2.7	6.1	5.9	3.4
Regulus regulus	3.9	2.1	3.8	2.1	2.4	2.6	2.2	4.2	4.7	4.2
Regulus ignicapillus	1.5		0.3		1.1	1.1	2.5	1.5	0.7	2.9
Sitta europaea	0.5			0.3				0.5		2.1
Certhia familiaris	2.7	3.2	2.1	2.1	2.4	2.9	2.7	3.9	2.7	3.9
Troglodytes troglodytes	4.7	5.9	5.4	2.9	2.4	7.4	5.7	2.1	2.2	5.4
Turdus philomelos	2.2	0.5	0.3	1.1	1.1		2.5	1.7	2.1	2.2
Turdus merula	0.7	0.5	0.5		0.3	0.7	0.2	2.1	0.5	2.7
Turdus torquatus	1.0		0.5		0.5	0.4	1.1	4.9	3.4	4.9
Erithacus rubecula	7.1	8.8	9.1	9.4	7.2	7.4	4.9	4.7	4.4	6.6
Phoenicurus phoenicurus								0.2		
Prunella modularis	5.4	3.4	2.4	3.8	3.2	5.5	5.2	12.1	4.9	1.7
Anthus trivialis	0.5					0.4		0.2	0.2	0.5
Fringilla coelebs	19.4	22.9	15.8	15.3	15.8	20.3	20.9	18.9	11.6	20.6
C. coccothraustes										0.2
Pyrrhula pyrrhula	2.1	3.2	1.9	0.8	3.8	1.8	1.5	1.5	1.2	1.2
Loxia curvirostra	2.5	1.2					1.1	1.7	3.4	3.2
Spinus spinus	0.7	0.5	0.5	0.5	1.1		0.7	1.2	0.2	1.1
No. of species	25	21	20	19	21	22	26	32	24	27
No. of breeding pairs	76.5	66.6	63.6	55.2	57.9	65.3	69.3	82.6	63.2	86.5

Tab. A5 Results of GLMMs testing for the effects of individual forest structural characteristics on Shannon diversity, species richness and abundance of bird assemblages. Likelihood-ratio test statistics (χ^2) and associated probabilities (p) are displayed. For explanation of shortcuts of structural variables see Tab. A3.

Structural variable	Shannon diversity		Species richness		Abundance	
	χ^2	p	χ^2	p	χ^2	p
missing bark	0.15	0.697	0.15	0.701	0.71	0.401
large DW	0.06	0.803	0.13	0.717	1.50	0.220
DW BA	0.59	0.444	0.76	0.384	1.81	0.178
DW volume standing	0.66	0.418	0.84	0.359	1.22	0.269
DW volume	0.43	0.510	0.59	0.443	1.63	0.202
canopy openness mean	1.04	0.309	1.01	0.315	0.72	0.395
vol_logs_all	< 0.01	0.952	< 0.01	0.993	0.81	0.367
dbh_quadrmean_dead_60	0.24	0.622	0.31	0.578	3.65	0.056
n_trees_live_500	0.35	0.555	0.50	0.478	1.79	0.181
n_trees_live_700	2.29	0.130	2.53	0.112	0.89	0.345
n_trees_dead_700	0.27	0.606	0.18	0.668	0.06	0.806
n_trees_dead_60	0.16	0.687	0.23	0.634	0.04	0.837
n_trees_live_60	0.01	0.909	< 0.01	0.962	< 0.01	0.974
dbh_mean_live_60	< 0.01	0.976	< 0.01	0.962	0.03	0.853
dbh_mean_dead_60	0.15	0.698	0.19	0.664	3.04	0.081
dbh_max_live_60	0.12	0.733	0.12	0.728	0.57	0.450
dbh_max_dead_60	0.13	0.718	0.25	0.614	3.98	0.046
age_5oldest	0.71	0.400	0.87	0.351	0.04	0.835
age_median	0.34	0.562	0.36	0.549	0.03	0.854
age_mean	1.38	0.240	1.56	0.212	0.08	0.777
openness_gini	1.88	0.170	1.95	0.162	2.19	0.139
sum_cavities10	0.73	0.392	0.87	0.352	0.07	0.788
sum_cracks60	0.18	0.670	0.19	0.667	0.02	0.901
sum_crowndeadwood70	1.35	0.246	1.30	0.255	0.52	0.469
sum_others80	1.30	0.254	1.54	0.215	1.56	0.212
trem_density_ha	0.99	0.319	1.12	0.290	0.05	0.828
regeneration_0_50	0.90	0.342	0.98	0.321	< 0.01	0.995
regeneration_250_100	0.81	0.367	0.70	0.402	0.01	0.943
regeneration_130_250	0.08	0.777	0.04	0.841	0.16	0.688
regeneration_50_130	0.60	0.439	0.58	0.446	0.03	0.865

Tab. A6 Fits of forest structural characteristics onto ordination plot of db-pRDA (Fig. 7). Goodness-of-fit measures (r^2) and associated probabilities (p) are displayed. Results significant at $\alpha = 5\%$ are highlighted in bold. For explanation of shortcuts of structural variables see Tab. A3.

Structural variable	r^2	p
missing bark	**0.10**	**0.034**
large DW	**0.14**	**0.034**
DW BA	**0.17**	**0.007**
DW volume standing	**0.17**	**0.004**
DW volume	**0.20**	**0.003**
canopy openness mean	**0.15**	**0.010**
vol_logs_all	0.09	0.144
dbh_quadrmean_dead_60	0.08	0.217
n_trees_live_500	0.06	0.149
n_trees_live_700	< 0.01	0.933
n_trees_dead_700	0.01	0.607
n_trees_dead_60	0.07	0.128
n_trees_live_60	0.05	0.188
dbh_mean_live_60	0.04	0.135
dbh_mean_dead_60	0.10	0.130
dbh_max_live_60	0.06	0.123
dbh_max_dead_60	< 0.01	0.906
age_5oldest	0.05	0.169
age_median	0.01	0.809
age_mean	0.02	0.656
openness_gini	< 0.01	0.855
sum_cavities10	0.02	0.395
sum_cracks60	0.02	0.494
sum_crowndeadwood70	0.02	0.452
sum_others80	0.02	0.269

trem_density_ha	0.04	0.159
regeneration_0_50	< 0.01	0.841
regeneration_250_100	0.03	0.593
regeneration_130_250	0.02	0.744
regeneration_50_130	0.01	0.772
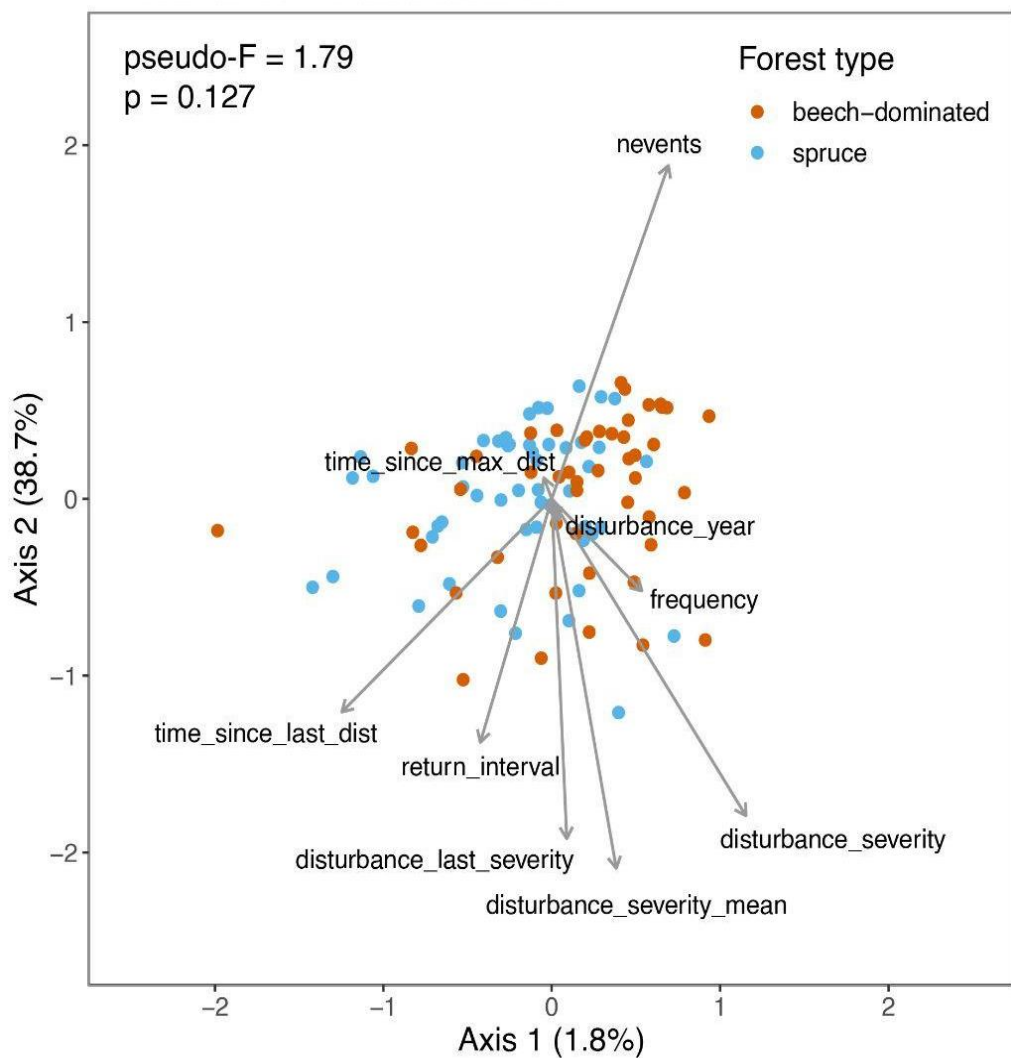
Fig. A5 Disturbance characteristics in beech- and spruce-dominated primary forests. Ordination diagrams show scores of sampling plots (dots) and vectors of environmental variables (arrows). The proportion of variance explained by the ordination axes is given in parentheses. The ordination plots are scaled symmetrically.

Tab. A7 All analysed structural variables with their description.

structural variable	Description	units
missing_bark	number of trees with bare wood patches with bark loss and wood in a decay stage of less than 2	number
n_trees_dead_500	density of the large dead trees (DBH ≥ 500 mm, height > 1.3 m) per hectare	number of stems per hectare
volume_dead_total	amount of lying and standing deadwood	m^3 / ha
openness_mean	mean openness calculated from the 6 hemispherical photos evaluated in WinSCANOPY	% of canopy area
volume_dead_lying	volume of lying deadwood with thickness on thinner end ≥ 100 mm	m^3 / ha
n_trees_live_500	density of the large living trees (DBH ≥ 500 mm) per hectare	number of stems per hectare
n_trees_ha	density of the living trees (DBH ≥ 60 mm) per hectare	number of stems per hectare
dbh_mean_live_60	mean diameter of the living trees (DBH ≥ 60 mm)	mm
age_5oldest	age of 5 oldest living trees (DBH ≥ 60 mm)	years
age_median	median age of living trees (DBH ≥ 60 mm)	years
age_mean	mean age of living trees (DBH ≥ 60 mm)	years
regeneration_250_100	density of the regeneration (height > 250 cm, DBH < 100 mm) per hectare based on the data of the plot	number of stems per hectare
regeneration_130_250	density of the regeneration (130 - 250 cm height) per hectare based on the data of the plot	number of stems per hectare
regeneration_50_130	density of the regeneration (50 - 130 cm height) per hectare based on the data of the plot	number of stems per hectare

Tab A8 Differences in bird community species recorded. Number of individuals in SDPF and BDPF were adjusted to account for different sampling effort.

species	Total abundance		Dominance [%]	
	beech	spruce	beech	spruce
Accipiter nisus	1	0	0.0	0.0
Aegithalos caudatus	2	0	0.1	0.0
Aegolius funereus	0	2	0.0	0.1
Anthus trivialis	2	6	0.1	0.2
Aquila chrysaetos	0	1	0.0	0.0
Bonasa bonasia	3	14	0.1	0.5
Buteo buteo	0	4	0.0	0.2
Carduelis spinus	1	27	0.0	1.0
Certhia familiaris	96	108	4.6	4.1
Cinclus cinclus	0	0	0.0	0.0
Coccothraustes coccothraustes	13	1	0.6	0.0
Columba oenas	14	0	0.7	0.0
Columba palumbus	23	15	1.1	0.6
Corvus corax	1	1	0.0	0.0
Cuculus canorus	2	18	0.1	0.7
Cyanistes caeruleus	3	0	0.1	0.0
Dendrocopos leucotos	26	0	1.2	0.0
Dendrocopos major	18	1	0.9	0.0
Dryocopus martius	4	3	0.2	0.1
Erithacus rubecula	215	257	10.3	9.8
Falco peregrinus	2	0	0.1	0.0
Falco tinnunculus	0	0	0.0	0.0
Ficedula albicollis	84	0	4.0	0.0
Ficedula parva	1	0	0.0	0.0
Fringilla coelebs	539	670	25.7	25.6
Garrulus glandarius	9	4	0.4	0.2
Glaucidium passerinum	0	5	0.0	0.2
Lophophanes cristatus	2	32	0.1	1.2
Loxia curvirostra	1	52	0.0	2.0
Muscicapa striata	12	0	0.6	0.0
Nucifraga caryocatactes	0	29	0.0	1.1
Parus major	38	0	1.8	0.0
Periparus ater	131	232	6.2	8.9
Phoenicurus phoenicurus	0	1	0.0	0.0
Phylloscopus collybita	172	155	8.2	5.9
Phylloscopus sibilatrix	42	0	2.0	0.0
Phylloscopus trochilus	43	31	2.1	1.2
Picoides tridactylus	2	43	0.1	1.7
Picus canus	2	0	0.1	0.0
Poecile palustris	3	0	0.1	0.0
Prunella modularis	54	180	2.6	6.9
Pyrrhula pyrrhula	23	71	1.1	2.7
Regulus ignicapilla	46	43	2.2	1.7
Regulus regulus	83	123	4.0	4.7
Scolopax rusticola	0	6	0.0	0.2
Sitta europaea	42	13	2.0	0.5
Strix aluco	1	0	0.0	0.0
Strix uralensis	1	0	0.0	0.0
Sylvia atricapilla	127	116	6.1	4.4
Sylvia curuca	0	0	0.0	0.0
Tetrao urogallus	0	6	0.0	0.2
Troglodytes troglodytes	102	158	4.9	6.0
Turdus merula	68	32	3.2	1.2
Turdus philomelos	65	53	3.1	2.0
Turdus torquatus	8	65	0.4	2.5
Turdus viscivorus	13	0	0.6	0.0